ORIGINAL ARTICLE

Nest-site selection of the Red-billed Leiothrix and Japanese Bush Warbler in Japan

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ORNITHOLOGICAL SCIENCE

Abstract The Red-billed Leiothrix *Leiothrix lutea* has been introduced from China and is rapidly increasing in deciduous broad-leaved forests of Japan. We studied nest-site characteristics and nest-site selection of this species and the Japanese Bush Warbler *Cettia diphone*, a sympatric native species, in southwestern Japan. Both species placed nests exclusively in bamboo thickets and on bamboo stalks. The Red-billed Leiothrix built pendulous nests in the canopy of high concealment. The Japanese Bush Warbler placed nests on the crossing of bamboo stems and selected places of high stem density. The Japanese Bush Warblers placed nests in denser vegetation than the Red-billed Leiothrix. The segregation of nesting microhabitat was also evident in both species to coexist in bamboo thickets. Existence of few inhabitants in bamboo thickets may contribute to the invasion success of the Red-billed Leiothrix.

Key words *Cettia diphone*, Introduced birds, *Leiothrix lutea*, Nest-site selection

Many birds have been transported out of their native ranges for trading, which has facilitated establishment of naturalised populations in various regions of the world (Long 1981). Biological invasion raises several ecological questions. First, what factors affect invasion success (Case 1991; Veltman et al. 1996). Second, what are the direct or indirect influences of introduced species on native species (Diamond & Case 1985; Lodge 1993). The second question is especially important for people who deal with the conservation of native avifaunas. In spite of its importance, there have been few studies on this subject, particularly during the establishment of introduced birds.

Introduced birds may diminish the number of native species through interspecific competition (Mountainspring & Scott 1985; Jones 1996). However, existence of interspecific competition is hard to detect (Lodge 1993), and evaluations of the influences of introduced birds on native ones have caused disputes (e.g. Moulton & Pimm 1983; 1986; Simberloff & Boecklen 1991; Simberloff 1992; Moulton 1993). It is important to clarify the ecological characteristics of both introduced and native species in order to discern the reasons for successful introduction and competition between them. A study of habitat selection is one approach to achieve this clarification (Sol et al. 1997).

Of forest-living birds which are believed to be less successful in establishment (Long 1981), two timaliidid species (Melodious Laughing-thrush *Garrulax canorus* and Red-billed Leiothrix *Leiothrix lutea*) and the Japanese White-eye *Zosterops japonica* have successfully established in native forests of Hawaii (Mountainspring & Scott 1985). The Red-billed Leiothrix has established also in deciduous broad-leaved forests of Japan in recent years (Yamashina Institute for Ornithology 1993; Eguchi & Masuda 1994). Notably, the same species have established in native forests of different regions which are believed to be resistant habitats to exotic birds.

The Red-billed Leiothrix ranged originally from southern China to the Himalayan region (Ali & Ripley 1972; Long 1987) and is a popular caged bird in Western countries. In Hawaii, North America and the European continent, naturalised populations have been reported (Long 1981; Lever 1987). In Japan, the number of naturalised individuals has been increasing rapidly in deciduous broad-leaved forests above

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1,000 m in elevation during the past two decades (Eguchi & Masuda 1994; Tojo 1994). However, information on the ecology of the Red-billed Leiothrix in natural habitat is generally lacking in native and introduced regions (but see Fisher & Baldwin 1947; Ralph et al. 1998).

In deciduous broad-leaved forests in Japan, the Red-billed Leiothrix forages in the lower layer of the forest and nests in thickets of dwarf bamboo (Eguchi & Masuda 1994). Only one sympatric species, the Japanese Bush Warbler *Cettia diphone*, nests in the same habitat where competition between them is likely. In Hawaiian islands, the Red-billed Leiothrix and Melodious Laughing-thrush diminished the number of native species through interspecific competition (Mountainspring & Scott 1985). Whether such an influence upon Japanese Bush Warblers has been exerted by the Red-billed Leiothrix is an important concern. Two major resources, nest-sites and foods, may be limiting, if competition exists. Our objective is to clarify characteristics and selection of nest-site in the two species and to determine the effect of nest-site microhabitat on nesting success. We discuss the possible impact of the Red-billed Leiothrix on native species with reference to the utilisation of nesting habitat.

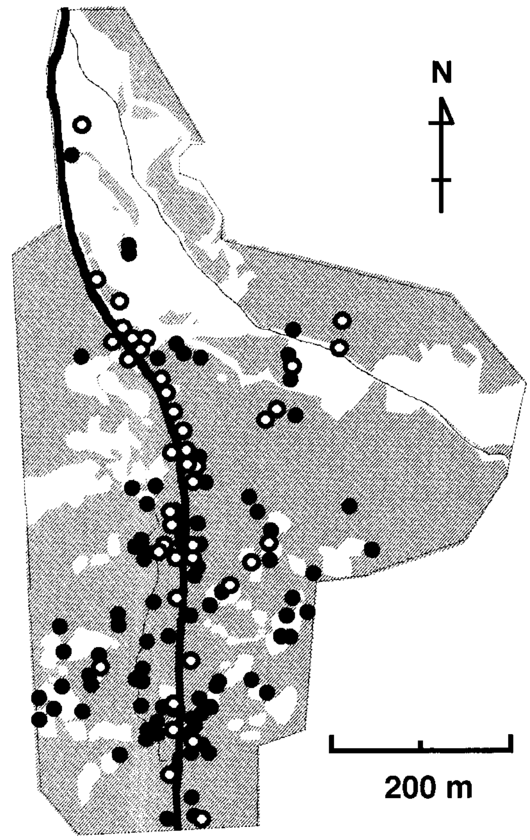

Fig. 1. Distribution of nests at a study site in 1998. Closed circles are the nests of Red-billed Leiothrix and open circles are those of Japanese Bush Warbler. The thick line is a road and thin lines are paths. All of the study area is covered with a continuous canopy of tall trees with dwarf bamboo (hatched areas) and bare ground (open areas) comprising the understory.

METHODS

The study was conducted from April to August, 1997–1999 in the Ebino Plateau, Miyazaki and Kagoshima Prefectures, southwestern Japan (1,200 m elevation; 31°56′N, 130°51′E). The main study area was a mixed forest (16 ha) composed of *Abies firma*, *Tsuga sieboldii*, *Pinus densiflora*, *Quercus crispula*, *Hydrangea paniculata*, *Symplocos coreana* and *S. myrtacea*. In the shrub layer, dwarf bamboo *Sasamorpha borealis* of ca. 2 m in height, was spread predominantly throughout the forest, with small patches of bare ground. A road of ca. 10 m in width ran through the forest (Fig. 1). In 1997, additional data were collected at a 6 ha site, 800 m northwest of the main study area. The vegetational structure in the second site was the same as in the main study area. 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). It was about twenty years since the Red-billed Leiothrix was first recorded in this area (Kamitanigawa pers. comm.).

Nests were located by systematic searches in the bamboo thicket, using song and behaviour of birds as a cue. Nests were marked with plastic flags. Nests were checked at 3–7 days intervals until failure or fledging. Chicks of both species fledge between 10 to 15 days after hatching (pers. obs.). If chicks disappeared during this stage, we searched for them around nest-sites to confirm whether they fledged or not. If at least one chick fledged, the nest was assigned as "successful". Because we could not distinguish between first and second nesting attempts for most nests, we combined them in the analyses.

After the termination of breeding, each nest was visited for measurement of nest-site characteristics. Variables measured were; size of nest, nest materials, nest height from the ground, height of bamboo canopy, length of the longest stalk supporting a nest, distance from the root of supporting bamboo to the nest, the number of twigs supporting a nest, the number of stems supporting a nest, distances from nearest stream, road, and edge of thicket, and density of vegetation. The density of vegetation was evaluated as follows. A red plastic board (25×40 cm) was placed 50 cm above the ground adjacent to the stalks supporting the nest, and a photograph of the board was taken from 1 m away. We scanned these photographs and measured the area of the red portion of the board using the public domain NIH Image program (developed at the U.S. National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/) on a Macintosh computer. The density of vegetation is indicated by the area of the board obscured by the vegetation (=1,000−the area of red portion of the board). In 1999, we did not conduct nest measurements.

The density of the bamboo thicket varied from relatively open to quite dense. In order to examine the relationship between the density of bamboo and distance from the road, we sampled bamboo density in ten 50×50 cm quadrats (2 quadrats sets 2 m apart at 10 m intervals) along a 50 m transect. Five and four transects were set east and west of the road, respectively. We counted the number of live bamboo stems in each quadrat. Data from two quadrats were summed for each point. Similarly, four transects were set parallel to the road between neighbouring streams.

Because the foliage of bamboo is concentrated around the terminal end of the stem, nests in the foliage are of low visibility while those in the middle of stem are of high visibility. In 1999, in order to examine the nest-site selection of both species, the stem density and the visibility index were measured at the nests and at control points. To quantify the stem density, we counted the number of stems in a quadrat of 50×50 cm. Three visibility indices were measured as follows. A white board (30×45 cm) with 5×5 cm grids was placed at heights of 1 m (approximate bush warbler nest level) and 1.8 m (approximate leiothrix nest level). At a distance of 1.5 m from the board, we counted the number of intersections visible with the naked eye or through a video camera. The index ranged from 0 (no visibility) to 54 (perfect visibility). In order to quantify the degree of visibility at height of 1.8 m (the level of bamboo canopy), we used two different indices, the one from a point 1 m above the ground and the other from a point 1.8 m above the ground. Control points were chosen at a distance of 10 m north of each nest. If the point chosen fell on bare ground, another point was chosen to the south of the nest.

Logistic regression analysis of data collected in 1999 was used to determine characteristics related to nest-site selection. The dependent variable was nominal: places preferred for nesting and control points. Independent variables were stem density and the three visibility indices.

Only completed nests were used for the analyses. Except for the interspecific comparison of the density of vegetation around nests and the analysis of nesting success, only data from the main study area were used. However, because all information was not always obtained for all nests, sample sizes were different among analyses. Means are shown with SD. A significant level is at $\alpha=0.05$.

RESULTS

1) Nest shape and nest attachment

Many more Red-billed Leiothrixs' nests were found than those of the Japanese Bush Warbler: 67 nests (49 at the main site and 18 at the second site) in 1997, 83 in 1998, and 84 in 1999 for the Red-billed Leiothrix, compared to 25 nests (17 at the main site and 8 at the second site) in 1997, 41 in 1998, 22 in 1999 for the Japanese Bush Warbler. New nests of the Red-billed Leiothrix were cup-shaped, 9.7±1.0 cm in diameter and 9.3±1.2 cm in height for 135 nests measured (data combined for 1997 and 1998) and were made of blades of bamboo, moss, roots of plants and, sometimes, plastic cords. Nests of the Japanese Bush Warbler were elliptical ball-shaped, 10.1±1.4 cm in diameter and 14.9±2.4 cm in height for 56 nests measured, and were made entirely of blades of bamboo. Both species placed nests on bamboo stalks in dense bamboo thickets. Only one nest of the Red-billed Leiothrix was found in the understory lacking bamboo and dominated by *Symplocos myrtacea*.

The Red-billed Leiothrix placed their nests in foliage at the top of bamboo stalks. Although the length of stalks ranged from 2 to 3 m, stalks bent due to the weight of the nest so the nest height fell in the range of 1–2.5 m above the ground (Table 1). Nests were hung at the forks of stems with roots of plants and plastic cords. Each nest was supported by two or three stems. In a few cases, only one stem supporting the nest. The Japanese Bush Warbler placed nests at the middle height of stems, 0.5–2 m from the ground. Nests were attached to four or five stem crossings and were held to the stems rather than tied. Therefore, more stems were necessary to support a nest of the

Japanese Bush Warbler than that of the Red-billed Leiothrix (Table 1). The nest height of Japanese Bush Warblers was lower than that of the Red-billed Leiothrix, though not significant, in 1997. However, this does not mean that the Japanese Bush Warblers preferred short bamboo thickets. The height of vegetation around the nests was not significantly different between these two species (Table 1). The Japanese Bush Warbler preferred nesting lower on the bamboo stalks than the Red-billed Leiothrix.

A high density of stems were necessary for the Japanese Bush Warbler to fasten the nest, while density of stems was not so important for the Red-billed Leiothrix. Many nests of Japanese Bush Warblers were located where the density of vegetation was high (Fig. 2). Mean values of indices of vegetation density were 743.9±107.0 (N=68) in 1997 and 529.9±157.7 (N=70) in 1998 for the Red-billed Leiothrix, and 808.5±116.3 (N=26) in 1997 and 604.8±148.6 (N=27) in 1998 for the Japanese Bush Warbler. In both years, Japanese Bush Warblers placed nests in denser vegetation than Red-billed Leiothrix ($U_{26,68}=572$, $P=0.01$ in 1997, $U_{27,70}=698$, $P=0.05$ in 1998; Mann-Whitney U-test).

Overlap in the spatial distribution of nests between both species was large (Fig. 1). However, nests of the Red-billed Leiothrix were distributed throughout the study area while those of Japanese Bush Warblers were concentrated near the road. The proportion of nests within 10 m of the road was greater for Japanese Bush Warblers than for Red-billed Leiothrix in both 1997 and 1998 (Table 2). Streams and bare ground also interrupted the bamboo thicket. The proportions of nests within 10 m of streams or bare ground were not different between the two species (Table 2).

The bamboo thicket was densest near the road (Fig. 3). However, there was not a consistent tendency between the density of bamboo stalks and the distance from a stream; 27.5±15.0 stalks per 5,000 cm^2 (N=13) within 10 m of a stream and 22.6±17.0 stalks (N=13) more than 10 m from a stream ($U_{13,13}=65.5$, $P>0.30$, Mann-Whitney U-test). Because tall trees were lacking near the road, the bamboo thicket grew well. However, because there was a continuous canopy of tall trees over the streams, the density of the bamboo thicket was not as high there, as near the road (27.5±15.0 stalks (N=13), versus 95.6±33.7 stalks (N=9), respectively, $U_{9,13}=0$, $P<0.0001$).

2) Nest-site selection

In the bamboo thickets, both species selected nest-sites non-randomly. Nests were placed at points of higher concealment and higher density of bamboo stems than control points by both species (Table 3).

Table 1. Comparison of nest placement between Red-billed Leiothrix and Japanese Bush Warbler.

		1997						1998					
		Red-billed Leiothrix		Japanese Bush Warbler				Red-billed Leiothrix		Japanese Bush Warbler			
	N	40		16				72		32			
		mean	SD	mean	SD	U	P[e]	mean	SD	mean	SD	U	P[e]
Height (cm)	Nest	165.8	34.7	146.9	27.3	232	>0.10	159.7	33.3	137.8	32.2	731.5	<0.01
	Bamboo	236.3	29.9	238.8	25.8	313	>0.80	218.8	41.5	220.9	34.8	1087	>0.60
Length (cm)	Nest[a]	—	—	—	—	—	—	214.4	38.5	142.2	37.6	219.5	<0.001
	Bamboo[b]	—	—	—	—	—	—	257.1	37.1	220.9	37.5	524.5	<0.001
Relative nest height[c]		3.8	0.5	3.0	0.6	112	<0.001	3.7	0.5	2.9	0.5	334	<0.001
Nest attachment[d]	Twig	6.3	2.3	6.1	1.6	314.5	>0.90	6.5	2.1	7.8	2.3	750.5	<0.01
	Stem	2.6	1.2	4.0	1.4	138	0.001	2.9	1.0	4.8	1.4	309.5	<0.001

[a] distance from the root of supporting bamboo to the nest
[b] length of the longest stalk supporting a nest
[c] divided into four portions (1st, 2nd, 3rd and 4th from ground to top)
[d] number of twigs (stems) supporting a nest
[e] Mann-Whitney's U test

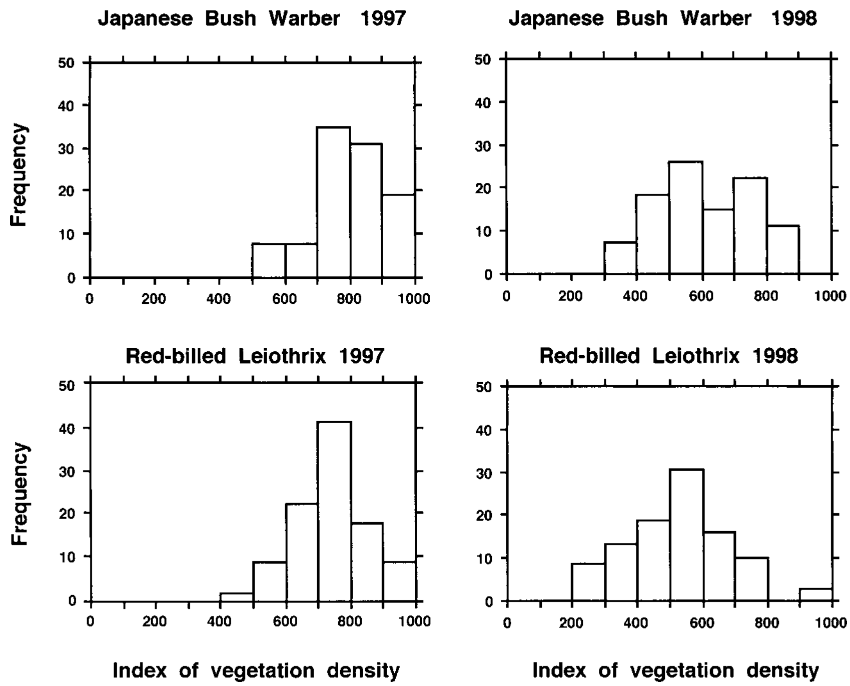

Fig. 2. Comparisons of the density of vegetation around nests between the Red-billed Leiothrix and the Japanese Bush Warbler. The index of vegetation density is shown as an area of a board covered with vegetation.

Table 2. Locations of nests of Red-billed Leiothrix and Japanese Bush Warbler.

		1997			1998		
		Red-billed Leiothrix		Japanese Bush Warbler	Red-billed Leiothrix		Japanese Bush Warbler
	N	50		18	77		36
Distance from road							
	Less than 10 m	6		10	21		26
	More than 10 m	44		8	56		10
	P[a]		0.001			<0.001	
Distance from bare ground							
	Less than 10 m	24		7	30		11
	More than 10 m	26		11	47		25
	P[a]		>0.50			>0.40	
Distance from streams							
	Less than 10 m	22		5	46		24
	More than 10 m	28		13	31		12
	P[a]		>0.20			>0.50	

[a] Fisher's exact probability-test

For Red-billed Leiothrix, the differences were significant for the stem density and visibility indices in the canopy but not for the visibility index at the lower height. However, logistic regression indicated that the overall contribution of these variables was low ($R^2=0.14$) and no particular characteristic was related to the separation between nests and control points (Table 4). On the other hand, the Japanese Bush Warbler selected high stem density and well concealed places. The density of bamboo stems and visibility index in the canopy were related to the separation between nests and control points (Table 4).

3) Nesting success and vegetation density at nest-site

In the Red-billed Leiothrix, fate of 51 nests was traced and five nests were successful (9.8%) in 1997, five from 63 nests (7.9%) in 1998, and only two from 68 nests (2.9%) in 1999, respectively. In the Japanese Bush Warbler, only one nest was successful from 18 nests (5.3%) in 1997, and no nest was successful in both 1998 (from 33 nests) and 1999 (from 14 nests). More than a half of nests studied were left no egg laid. In the Red-billed Leiothrix, the proportions of nests in which eggs were laid were 43.1% (=22/51), 34.9% (=22/63), 39.7% (=27/68), in 1997, 1998 and 1999, respectively. In the Japanese Bush Warbler, the proportions of nests in which eggs were laid were 50.0% (=9/18), 36.4% (=12/33), 21.4% (=3/14), in 1997, 1998 and 1999, respectively. We could not determine whether these failed nests were deserted before clutch initiation or were depredated soon after that. Most failures after clutch initiation were due to total loss of clutches or broods, which suggests nest predation. Combined data for three years: 58 of 59 nests in which causes of failure were confirmed in the Red-billed Leiothrix and 20 of 23 nests in the Japanese Bush Warbler. We observed the Jay *Garrulus glandarius* and snakes (species unknown) predating nestlings.

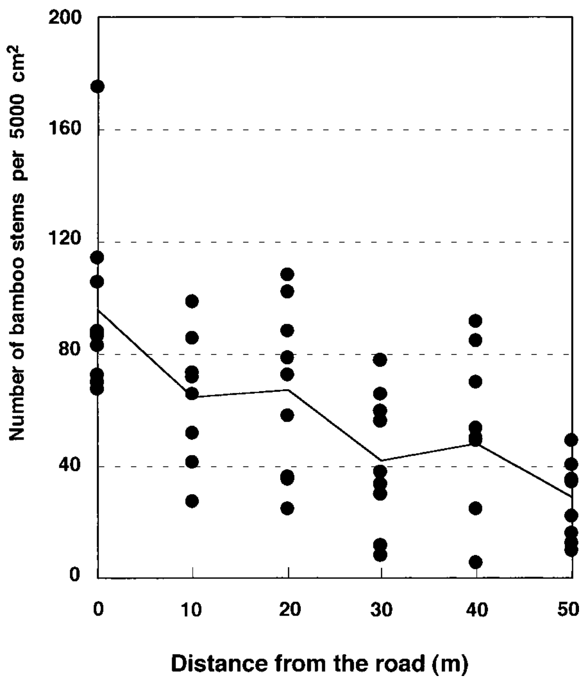

Fig. 3. The relationship between the density of bamboo stems and distance from the road. The line connects means.

In the Red-billed Leiothrix, neither the density of vegetation nor nest height related to nesting success. The indices of vegetation density of the successful nests and failed nests were 769.9±166.8 vs. 740.8±101.9 in 1997 ($U_{5,42}$=83, P>0.40; Mann-Whitney U-test), 586.3±224.2 vs. 528.8±147.3 in 1998 ($U_{5,49}$=90, P>0.30) and the nest height were 174.0±48.3 cm

Table 3. Comparison of the stem density and the visibility index between nests and control points for Red-billed Leiothrix and Japanese Bush Warbler.

		Red-billed Leiothrix		Japanese Bush Warbler	
	N	31		22	
		mean	SD	mean	SD
No. of stems	Nest	27.6	13.9	38.3	11.4
	control	19.7	12.5	23.1	11.5
	P[a]	<0.05		0.001	
Visibility index					
1 m above ground	Nest	16.4	10.3	13.3	7.6
	control	21.5	11.3	18.4	10.0
	P[a]	>0.10		<0.05	
canopy from below	Nest	5.4	4.1	5.6	6.9
	control	9.6	6.7	8.0	6.6
	P[a]	<0.05		<0.05	
canopy level	Nest	4.4	4.2	3.1	3.3
	control	8.8	7.6	8.2	8.0
	P[a]	<0.01		0.001	

[a] Wilcoxon's signed-ranks test

Table 4. Logistic regression analysis of the stem density and the visibility index between nests and control points for Red-billed Leiothrix and Japanese Bush Warbler.

	Red-billed Leiothrix		Japanese Bush Warbler	
N	62		44	
Characteristics	Parameter estimate	P	Parameter estimate	P
Intersect	−0.77	0.53	2.64	0.15
Density of stems	−0.02	0.48	−0.11	0.01
Visibility index at 1 m above ground	0.01	0.72	0.01	0.93
Visibility index in canopy from below	0.08	0.29	−0.13	0.14
Visibility index in canopy	0.07	0.29	0.27	0.04
	$R^2=0.14$		$R^2=0.36$	

vs. 162.9±32.5 cm ($U_{5,42}=90$, $P>0.60$ in 1997), 152.0±32.7 cm vs. 156.1±31.3 cm in 1998 ($U_{5,49}=98$, $P>0.40$; Mann-Whitney U-test). In the Japanese Bush Warbler, sample sizes of nesting success were too small to test.

In 1999, because few nests were successful, we could not show the relationships between nesting success and nest characteristics (the stem density and indices of visibility).

DISCUSSION

1) Utilisation of bamboo thickets

The Red-billed Leiothrix builds nests on bamboo not only in the Ebino Plateau but also in other areas of Japan (this study; Nakamura & Tojo unpubl.; Eguchi & Amano unpubl.). Only a few species are known to nest in bamboo thickets in Japan, including the Japanese Bush Warbler, Grey Bunting *Emberiza variabilis*, Siberian Meadow Bunting *E. cioides*, Bull-headed Shrike *Lanius bucephalus* and the Japanese White-eye (Kiyosu 1951). In Mt. Tsukuba, Ibaraki prefecture, the Japanese Bush Warbler, Japanese White-eye, Siberian Meadow Bunting and Long-tailed Tit *Aegithalos caudatus* nest in thickets of bamboo *Sasamorpha borealis* (Nakamura & Tojo unpubl.). On the Kayanodaira Plateau, Nagano Prefecture, the Japanese Bush Warbler and Grey Bunting are the dominate nesting species in thickets of dwarf bamboo *Sasa senanensis* and *S. kurilensis* (Ezaki pers. comm.). However, only two native species, the Japanese Bush Warbler and Grey Bunting, nest predominantly in bamboo thickets in Japan. Although the avifauna is rich in deciduous broad-leaved forests, it is likely that the microhabitat which the Red-billed Leiothrix uses for nesting has been vacant.

The Red-billed Leiothrix is not a specialist nesting on bamboo stalks in its original habitats (Ali & Ripley 1972; Long 1987). In Hawaii, Red-billed Leiothrix nests in dense undergrowth, but does not specialise in a particular substrate tree species (Fisher & Baldwin 1947). Also in Japan, there have been a few cases where Red-billed Leiothrix nested on shrub trees, such as *Symplocos myrtacea*, *Abies firma*, *Eurya japonica*, *Litsea glauca*, and *Camellia japonica* (Eguchi & Amano unpubl.). The Monk Parakeet *Myiopsitta monachus*, a habitat generalist in its original range, became a specialist nesting solely on palms of *Phoenix* sp. in Spain (Sol et al. 1997). Sol et al. (1997) suggested that the preference of a habitat occupied by no other species allows the parakeet to increase rapidly in the initial stage of invasion and that gradually it expands the width of habitat preference after successful establishment. The Red-billed Leiothrix also could increase in number by nesting in bamboo thickets where few competitors live and by specializing in nesting substrate and position of the nest.

2) Difference in nest-site selection

Both the Red-billed Leiothrix and Japanese Bush Warbler selected dense vegetation for nesting. However, the species selected different nesting microhabitats. Red-billed Leiothrix built nests in the canopy of bamboos, while the Japanese Bush Warbler placed nests at the middle height of stems. Such a difference may be due primarily to a difference in manner of nest attachment between two species.

The Red-billed Leiothrix built pendulous nests at the top of bamboo stalks, while Japanese Bush Warblers built nests at the crossing of bamboo stems. Japanese Bush Warblers require a bamboo thicket of high density for fastening nests firmly. Therefore, nests of Japanese Bush Warblers are distributed in the vicinity of the forest edge, such as near roads where the bamboo thicket is densest. On the other hand, because the density of bamboo stalks is not important for attaching nests, the Red-billed Leiothrix selects a wider range of understory density for nest-sites than the Japanese Bush Warbler.

The Japanese Bush Warbler also places nests in the middle of the bamboo stem in other regions of Japan. On the Kayanodaira Plateau where the Red-billed Leiothrix has not invaded yet, the Grey Bunting places nests at the top of bamboo stalks in areas of relatively sparse thickets, while the Japanese Bush Warbler nests in denser thickets (Ezaki pers. comm.). Thus, two species with different nest-site preferences could coexist in bamboo thickets.

3) Nest-site selection and nesting success

Dense vegetation may provide shrub-nesting species excellent protection against predators and non-random nest-site selection has been found in other such species (e.g. Black-throated Blue Warbler, Holway 1991; Hooded Warbler, Kilgo et al. 1996; Wood Thrush, Hoover & Brittingham 1998). The Japanese Bush Warbler selected places of high stem density. Dense bamboo stalks may impede the movement of predators. The Red-billed Leiothrix placed nests in the canopy of bamboos of high concealment. However, logistic regression suggested that this species may not always select a place of highest concealment in a territory for nesting. The Red-billed Leiothrix sometimes built an exposed nest just above a stream. Apparently, nest concealment is not a primary factor determining nest-site selection in this species.

Although the Red-billed Leiothrix and Japanese Bush Warbler selected somewhat of nest-site characteristics, the nesting success was very low in these species due to predation, particularly evident in almost all nests of the Japanese Bush Warbler. The density of vegetation at the nest site and nest height did not influence nesting success. We observed nest predation by the Jay and snakes (species unknown). Another potential predator may be the Jungle Crow *Corvus macrorhynchos*. Avian predators such as corvids depend on visual cues, and activities of parent birds may be important cues for such predators (Holway 1991; Hoover & Brittingham 1998). We often observed jays flushing from canopies of bamboos. Some jays may have searched exclusively for nests of birds nesting in the bamboo thicket when eggs and nestlings of these species were available. On the other hand, snakes search for nests using olfactory cues (Burhans & Thompson 1998). The effect of nest-site characteristics to predation may vary depending on the predator species. If a guild of predators is composed of species searching in different ways, selection of a specific type of nest-site may not be advantageous (Filliater et al. 1994; Hoover & Brittingham 1998). High nest predation and failure to detect a significant relationship between nesting success and nest characters in this study may be due to a varied predator community.

Moreover, because the Red-billed Leiothrix is a newcomer in this area, there may have not been enough time for a counter adaptation against a new guild of predators to appear. However, this species renested rapidly after predation and breeding season was long, with egg-laying occurring from April to September (pers. obs.). Rapid renesting and a long breeding season may be adaptations to high nest predation as reported in other shrub-nesting species (Martin 1995). Further studies evaluating a role of each taxonomic group of predators on mortality of birds nesting in the bamboo thicket are needed.

4) Influence on breeding of the Japanese Bush Warbler

So far, no distinct influence of the Red-billed Leiothrix on native species, such as a decline in number or habitat shrinkage, has yet been reported. The locations of nests in the bamboo thicket differ between the Red-billed Leiothrix and Japanese Bush Warbler. Even in the case where nests of these species were close to each other, direct interaction suggesting interspecific territoriality was not observed. It is unlikely that competition for nest-sites occurs between these species.

However, indirect interference competition is probable. In the community of *Acrocephalus* warblers in the reed beds of Europe, such an increase of predation due to the coexistence of species of similar nest-site preference is also considered probable (Hoi et al. 1991).

When we searched for nests of the Red-billed Leiothrix, nests of the Japanese Bush Warbler were also found. A high density of nests may attract various kinds of predators into the breeding areas. In this study, the density of Red-billed Leiothrix nests, which was two to three times higher than that of Japanese Bush Warblers, may have caused an increase in the number of predators and predation on nests of shrub-living species (the functional response; Holling 1959). The breeding success of Japanese Bush Warbler may be low due to indirect interference competition caused by the increase of Red-billed Leiothrix. Further studies are needed including a monitoring in an area of initial invasion or eliminating experiments for the Red-billed Leiothrix.

The Red-billed Leiothrix has invaded various regions of the world (Long 1981). Comparisons of habitat selection among naturalised populations and among naturalised populations and populations in their original range may indicate flexibility of habitat preference in this species, as well as changes in habitat selection during the process of invasion. Further studies are needed both in the original and new habitats of the Red-billed Leiothrix .

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