

**Conservation and Management of Bird Species Diversity in  
Japanese Cool-temperate Broad-leaved Deciduous Forests**

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**Conservation and Management of Bird Species Diversity in  
Japanese Cool-temperate Broad-leaved Deciduous Forests**

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## **Chapter 1 General Introduction**

## **Chapter 1 General Introduction**

The preservation of biological diversity is one of the most important priorities of sustainable forest management, which is a worldwide issue for forestry. Up to the present, forests of the world have been destroyed and converted to other uses, resulting in serious consequences for regional and global biodiversity (Kittredge 1996). Forests cover about two-third of the total land area of Japan, and approximately 53 % of the forests are classified as natural (including secondary) forests and 41 % are plantations, with the remaining 4 % being logged forests, bamboo forests, and so on (Forestry Agency of Japan 2009). Therefore, management of planted forests, as well as natural and secondary forests, is important for preserving biological diversity of Japan.

Birds are useful indicators of forest biodiversity, because they are diverse and sensitive to changes within the forest environment, their classification and systematics are well established (e.g., Furness and Greenwood 1993), and standardized monitoring methods are available (e.g., Koskimies and Väisänen 1991, Bibby et al. 2000). On the other hand, birds have disadvantages, too. Their long lifespan may make it more difficult to monitor short-term changes and their superior ability of movement may obscure the spatial scale they represent (Furness and Greenwood 1993).

More than 10,000 bird species are recognized in recent classification (del Hoyo and Collar 2016), and 633 species have been recorded in Japan (The Ornithological Society of Japan 2012). However, serious deterioration in bird species diversity during these decades have been documented in various areas of the world (e.g., Askins et al. 1990, Böhning-Gaese and Bauer 1996, Fuller et al. 2005, Hewson et al. 2007), including Japan (Higuchi and Morishita 1999, Ministry of the Environment of Japan 2004, Amano and Yamaura 2007). Many birds are

higher-order predators in the forest ecosystems they live, and contribute to various ecosystem services, such as pollination, seed dispersal and excavating cavities (Whelan et al. 2015, Şekercioğlu et al. 2016).

Several types of natural forests are distributed through the Japanese archipelago and cool-temperate broad-leaved deciduous forest is one of the typical natural forest types found in Japan (Numata 1974). This forest type also presents in Europe and in North America, and holds similar problems for preserving forest bird diversity (Askins 2014).

Here, I describe three threats to bird species diversity in broad-leaved deciduous forests: 1) loss of primeval forests, 2) forest fragmentation, and 3) alien species invasion. Without understanding these issues, appropriate plans for sustainable forest management cannot be proposed.

### **Loss of primeval forests**

To date, most Japanese natural forests have been cut and converted to secondary and artificial forests from ancient times (Totman 1989). Remaining primeval or old-growth forests have been diminished and fragmented into small remnants due to human activities (Fukamachi et al. 1996). The loss of primeval forests causes a problem in management of bird diversity, because bird community dwelling in remnant primeval forests represents the original biodiversity of the ecosystem, which is a general goal of forest management for biodiversity. As no primeval forest has survived in Britain, for example, prehistoric conditions of bird communities in British woods could only be assessed from those in the Polish Białowieża Forest (Wesołowski 2007). Thus, the examination and documentation of bird communities in Japanese primeval and old-growth forests of each forest type, as well as their variations within a forest type, are urgent issues.

As many bird species migrate, bird species diversity of a forest changes seasonally, which makes it difficult to evaluate bird diversity based on data obtained only in a specific season. The Japanese archipelago forms a particular migration route of the East Asian Flyway (Yong et al. 2015), and each natural forest type of Japan harbors different sets of bird species (e.g., Yui 1976, Kanai et al. 1996, Tojo 2007). Migratory bird populations can be affected not only by the conditions of the breeding site, but also those of the wintering and stopover sites (Newton 2004, 2006). Considering that Japanese forests generally provide breeding habitats for tropical migrants and wintering habitats for migrants breeding in Siberian forests, information about the seasonality of bird communities is essential for conservation of bird diversity along the migration route. However, few studies have been conducted on the seasonal changes of bird communities throughout the year in natural or old-growth forests. Therefore, the seasonality of bird communities in Japanese primeval and old-growth forests is necessary for appropriate management of bird diversity.

### **Forest fragmentation**

Up to the present, about 40 % of Japanese forests have been converted to conifer plantations (Forestry Agency of Japan 2009), and these plantations, as well as secondary broad-leaved forests, have been managed in relatively small forest patches. Thus, those forests typically show a resultant fine mosaic that consists of conifer plantations and secondary forests of various ages, a traditional Japanese rural landscape, so called “Satoyama” (Takeuchi 2001, Takeuchi et al. 2003).

Although such semi-natural mosaic landscapes of Satoyama have contributed to conservation of biodiversity (e.g., Yui and Ishii 1994, Yamagawa et al. 2009), changes in lifestyle of Japanese people have affected on the preservation of such traditional landscapes.

The fuel revolution and the spread of chemical fertilizers have caused the abandonment and degradation of secondary forests (Washitani 2001, Takeuchi et al. 2003). Despite the fact that more than half of plantations are ready to be harvested, forestry in Japan has been stagnant due to its low profitability (Forestry Agency of Japan 2015). As a result of the low harvesting rate, Japanese forests are continually matured. Many species of various taxa, including some tropical migrants, which were once common in rural landscapes several decades ago are now included in the national or local red lists (Washitani 2001). To preserve bird species diversity in those landscapes, we need to understand the effects of stand age and type on it.

### **Alien species invasion**

Invasion by alien species is one of most serious threats for many birds (Birdlife International 2000). Besides native birds have directly suffered alien predators (Lever 1994), alien bird species could become a problem to the biodiversity of the area where they invaded (Long 1981, Lever 2005, Blackburn et al. 2009). Before 1980's alien birds in Japan generally have not invaded forest areas, except the Bamboo Partridge *Bambusicola thoracicus*. During these decades, however, several exotic Timaliidae species, such as the Red-billed Leiothrix *Leiothrix lutea*, the Chinese Hwamei *Garrulax canorus* (Kawakami and Yamaguchi 2004), the Masked Laughingthrush *G. perspicillatus* (Nakamura et al. 1993), the White-browed Laughingthrush *G. sannio* (Tojo et al. 2004) and the Moustached Laughingthrush *G. cineraceus* (Hamada et al. 2006), have invaded Japanese forest areas. The Red-billed Leiothrix has become dominant even in natural or old-growth deciduous forests (Eguchi and Masuda 1994, Eguchi and Amano 2004). However, its ecology and effects on native bird species have not yet been understood.

In this thesis, I conducted four field surveys to explore these three issues for preserving forest bird species diversity in Japanese cool-temperate deciduous forests. At first, I describe the characteristics of bird communities of the Ogawa Forest Reserve (OFR), a remnant old-growth deciduous forest in Ibaraki Prefecture, central Japan. I conducted monthly bird censuses using the point-count method to document the seasonality of bird communities in the OFR and compared it with those in other forest types (Chapter 2). I then surveyed breeding birds using the territory-mapping method for five years to document and characterize the breeding bird community of the OFR (Chapter 3). Next, I surveyed birds by the point-count method in 21 study plots set in a landscape of fine mosaic with various forest patches to examine the effects of stand age and type on the bird diversity (Chapter 4). To examine the effects on the native bird community of the Red-billed Leiothrix, which has invaded Japanese deciduous forests, I set an 8-ha plot on the north slope of Mt. Tsukuba, Ibaraki Prefecture, central Japan, and surveyed the breeding density of Leiothrix and native bird species by the territory-mapping method (Chapter 5). In the general discussion, I discuss the results for the three issues and propose some recommendations for the conservation of forest bird diversity (Chapter 6).

## **Chapter 2 Seasonality of the Bird Community in the Ogawa Forest Reserve, an Old-growth Deciduous Forest in Central Japan**

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## **Chapter 2 Seasonality of the Bird community in the Ogawa Forest Reserve, an Old-growth Deciduous Forest in Central Japan**

### **2-1 Introduction**

The conservation of migratory bird species is an urgent yet difficult issue because, unlike resident species, not only the conditions of the breeding site, but also those of the wintering and stopover sites can affect migrants (Newton 2004, 2006). Population declines in tropical migrant species prevails worldwide, as documented in North America (Terborgh 1989, Askins et al. 1990), Europe (Böhning-Gaese and Bauer 1996, Fuller et al. 2005, Hewson et al. 2007) and Japan (Higuchi and Morishita 1999, Amano and Yamaura 2007) during these decades. However, numerous studies have revealed that the avian ecology differs between migrating systems in: distribution patterns (Hino 1990, Newton and Dale 1996a, Newton and Dale 1996b, Newton 2003), habitat preferences (Mönkkönen and Helle 1989, Mönkkönen et al. 1992), sensitivity to habitat fragmentation (McLellan et al. 1986, Lampila et al. 2005), perhaps reflecting differences in the climatic conditions (Newton 2003), the history of clear cutting and disturbance (McLellan et al. 1986, Mönkkönen and Welsh 1994, Lampila et al. 2005), and the effects of glacial events during the Pleistocene (Hino 1990, Mönkkönen and Welsh 1994). Thus, worldwide recommendations cannot be made for planning a conservation strategy for migrants (Mönkkönen and Helle 1989), instead regional recommendations are necessary.

The East Asian-Australasian Flyway supports great diversity and large populations of migratory birds, but it is also one of the most poorly understood migration systems (Rappole 1996, Newton 2008, Yong et al. 2015). Because of its insular geography, more species have small breeding ranges and/or are dependent on tropical forests as wintering habitat than those in any other Eurasian migrating system, and are thus more vulnerable to habitat loss and

degradation throughout their ranges (Yong et al. 2015). In the East Asian-Australasian Flyway, unlike shorebirds, only certain land bird migrant species reach New Guinea and Australia as regular wintering species (Newton 2008, Yong et al. 2015). Consequently, a term “the East Asian Flyway” may be more appropriate, at least in the context of songbirds (Yong et al. 2015).

The Japanese archipelago forms a particular migration route of the East Asian Flyway. Several types of natural forest are distributed through the Japanese archipelago (Numata 1974) and these harbor different sets of bird species (e.g., Yui 1976, Kanai et al. 1996, Tojo 2007). Considering that these forests provide breeding habitats for tropical migrants and wintering habitats especially for granivorous migrants (Yong et al. 2015), information about the seasonality of bird communities is essential for conserving these migrants. However, few studies have been conducted on the seasonal changes of bird communities throughout the year, especially in natural or old-growth forests. Most census work on birds has been conducted during the breeding season when various breeding activities (e.g. singing, territorial behavior, nesting) provide reliable cues for estimating bird abundance (Emlen 1971, Bibby et al. 2000), and only rarely during the non-breeding season when many bird species are silent, cryptic, and sometimes nomadic. Although some studies have surveyed non-breeding bird communities over short periods (e.g., Yui 1977, Inoue and Hashizume 1990, Eguchi et al. 1992, Yamaura et al. 2008, Yamaura et al. 2009), as well as corresponding data in the breeding seasons (e.g., Inoue and Kondo 1983, Eguchi et al. 1989), the timing of the censuses during non-breeding season differs between studies (from November to March).

Cool-temperate, broad-leaved deciduous forest is one of the typical natural forest types found in Japan (Numata 1974) and the foliage dynamics of such forests contribute significant seasonality regarding the physical environment for birds. Although the bird communities in primeval or old-growth deciduous forests have been documented during the breeding season by

many studies (see Nakamura 1977, Chapter 3), the seasonality of such communities has not been studied as much, partly because heavy snowfall inhibits access to those forests in mountainous areas in winter (e.g., Ueuma 1979). Given the clear seasonality of this forest type, there should be a characteristic seasonal pattern in bird species diversity.

The Ogawa Forest Reserve (OFR) is an old-growth deciduous forest where intensive research has been conducted on the ecology of the tree community since 1987 (Nakashizuka and Matsumoto 2002). The bird community in the OFR has been documented during the breeding season (Chapter 3), but not during the non-breeding season or for its seasonality. This study aims to document the seasonality of the bird community in the OFR and characterize it in comparison with the seasonality in other types of Japanese forest.

## 2-2 Study Site and Methods

The Ogawa Forest Reserve (98 ha; 36°56′ N, 140°35′ E, 550–720 m a.s.l.) is located in the southern part of the Abukuma Mountains in central Japan. A 6-ha permanent plot for studying plant community dynamics has been established in the central part of the OFR (Tanaka and Nakashizuka 2002). The total basal area of stems in the plot is approximately 29 m<sup>2</sup>/ha, and the plot is dominated by *Quercus serrata* (26% of total basal area), *Fagus japonica* (21%), and *F. crenata* (9%). In terms of density, the dominant species are *F. japonica*, *Styrax obassia*, *Carpinus laxiflora*, *C. cordata*, and *Acer palmatum* var. *amoenum*. A shrub layer and dense patchy undergrowth of dwarf bamboo (*Sasa nipponica*, *Sasaella ramosa* and *Sasamorpha borealis*) are found in some portions of the OFR, but the herbaceous layer is generally scarce (Masaki et al. 1992).

I used the fixed-radius point-count method (Hutto et al. 1986, Bibby et al. 2000) for surveying a 12-ha plot (400 × 300 m, 620–680 m a.s.l.). The plot had been established so as to

include the 6-ha plot for plant dynamics, and was used for the territory mapping method for breeding bird surveys (Chapter 3). A major advantage of the point count method over the line transect method is the effective detection of visual cues because, unlike during a line transect, researchers need not watch their step (Reynolds et al. 1980). Thus, the point count method seems effective especially during the non-breeding season, when singing activity is low and researchers must depend more on visual cues than during the breeding season.

First, I set up twelve circular 50 m radius plots within the 12-ha plot (Fig. 2-1). The total area of the twelve circles was 9.42 ha and covered 78.5% of the original 12-ha plot. I recorded all birds and their distances during a 10 minutes stay at the center of each circle, including those recorded outside the circle as in the variable circular method (Reynolds et al. 1980), but in analysis, only records within the circle were used. The birds recorded in a day were simply summed up and converted to birds/10 ha. Bird cues that did not allow for species identification were omitted from this analysis.

Monthly census trips were made from September 1996 to August 1997. During the assumed peak of autumn migration in October and November, two censuses were carried out, in the early and late periods of each month. The census trips began from 04:55 to 07:09 (depending on the time of sunrise in the season), and took, on average, three hours and 20 minutes to complete the censuses for all 12 circular plots. The order of visiting the circles was fixed with consistent bias given in census time between the circles, but consistent relative to date. The census is intended to give an estimate of the bird assemblage in the 12-ha plot, not to compare data among the circles.

To evaluate the variability of seasonal bird communities, monthly census data were ordinated with non-metric multidimensional scaling (NMDS). I used a software package R version 2.15.2 (R Development Core Team 2012) and R packages ‘vegan’ for multivariate

analysis of ecological communities (Oksanen 2013) and 'MASS'. NMDS by the metaMDS function in vegan uses Bray-Curtis dissimilarity distances among the sites as default, and seeks to determine the optimum position of n entities in k-dimensional space, so as to minimize a statistic called 'stress' that reflects how well the configuration represents the distances. I compiled a data matrix with bird species as columns and the sampling time of the year, instead of sampling sites, as rows. I designated the "breeding season" to be from April to August, and the "non-breeding season" from October to February. March and September were designated as the "transition season" when certain resident species begin or continue breeding activity.

The position of sampling times and bird species were plotted on a two-dimensional space. For the sampling times in each season, an enclosing convex hull was drawn using a utility function "ordihull" in vegan. To abbreviate the scientific names of birds the function "make.cpnames" was used. The taxonomy and nomenclature is based on the check-list of Japanese birds 7th revised edition (The Ornithological Society of Japan 2012).

## **2-3 Results**

### **2-3-1 Species richness and abundance**

Of the 61 bird species observed in the OFR during the study, 41 species were recorded by the point count method in the survey plots (Table 2-1). Monthly species richness varied from 6 in January to 21 in April (Fig. 2-2). On the census day in January, shallow snow covered most of the ground surface and might have been partially responsible for the poor bird diversity.

Total bird abundance fluctuated from 25 birds/10 ha in January to 138 birds/10 ha in April (Fig. 2-3). Tits (Paridae), long-tailed tits (Aegithalidae), and woodpeckers (Picidae), were dominant throughout the year. Thrushes (Muscicapidae) were also observed throughout the year, but species varied seasonally as this group includes summer visitors (e.g. Japanese Thrush

*Turdus cardis*), transients (e.g. Eyebrowed Thrush *Turdus obscurus*), and winter visitors (e.g. Naumann's Thrush *Turdus naumanni*). During the breeding season, some species of flycatchers (Muscicapidae) and minivets (Campephagidae) were added to the assemblage. Conversely during the non-breeding season, such seed-eaters as finches (Fringillidae) and buntings (Emberizidae), and such fruit-eaters as thrushes and waxwings (Bombycillidae) were observed until December, but largely disappeared by January.

As for migration status, the species richness of such resident species as tits, long-tailed tits, and woodpeckers accounted for more than half of all species throughout the year (Fig. 2-2). Summer visitors accounted for up to 33% (7/21) of all species in April. Winter visitors accounted for 27% (4/15) in December, but were not recorded in January and February. As transient species, only a few Eyebrowed Thrushes were recorded in autumn.

The abundance of permanent residents was also high throughout most of the year (Fig. 2-4). Summer visitors accounted for 10 to 27% during the breeding season (April–August), but were never dominant when compared with permanent residents in abundance. During the non-breeding season, winter visitors temporarily accounted for 72% in December when Japanese Waxwings *Bombycilla japonica* were observed in flocks, but were not recorded in January.

### **2-3-2 Ordination**

A non-metric multidimensional scaling ordination divided bird assemblages into breeding season (April–August) and non-breeding season (October–February) clearly (Fig. 2-5). September was positioned as the intermediate region of both seasons, with March falling within the non-breeding season. The bird communities during the breeding season were concentrated in a relatively small area compared to those during the non-breeding season. This suggests that the

bird community in the OFR was relatively stable during the breeding season, but variable during the non-breeding season.

Tropical migrants, such as Blue-and-White Flycatchers *Cyanoptila cyanomelana* and Ashy Minivets *Pericrocotus divaricatus*, were plotted near the breeding season group, whereas winter visitors, such as Red-flanked Bluetail and Rustic Bunting *Emberiza rustica*, fell within the non-breeding group. Resident species were plotted elsewhere between the two seasons, depending on the seasonal bias in appearance. The temporarily observed species, such as Japanese Waxwings in December and Grey Buntings *Emberiza variabilis* in late October, were plotted in remote areas in the space and contributed to the large variation in the monthly assemblages during the non-breeding season.

## **2-4 Discussion**

### **2-4-1 Seasonal pattern of bird diversity in Japanese cool-temperate forests**

The seasonality of the bird community in the OFR showed relatively high diversity in both breeding and autumn migration seasons, and a trough in mid-winter in both species richness and abundance. Although the resident species in the OFR dominated throughout the year, tropical migrants and winter visitors characterized the breeding and the non-breeding assemblages, respectively. While the tropical migrants stayed during the breeding season, winter visitors replaced each other even within a single season.

The decline in mid-winter was partly due to the disappearance of winter visitors in January. Similar declines in bird diversity following snowfall in mid-winter have been observed in other areas of Japan (e.g., Oka and Nakamura 1998). As winter visitors that disappeared were not recorded even in February or March, when the ground cover of snow had thawed, they are

considered to have left the OFR. In contrast, residents more or less returned by March, indicating that part of the population had moved, temporarily, to surrounding areas.

In another Japanese cool-temperate forest on Mt Takasaburo (Ishikawa Prefecture; 36°22' N, 136°46' E, 1421 m a.s.l.) with a harsh winter climate, the seasonality of bird diversity showed a similar pattern, but the range of the decline in winter was larger than that in the OFR (Ueuma 1979). Species richness peaked in May (56) and was lowest in December (13) and March (12), although data were lacking for January and February due to heavy snow. In considering the climatic conditions, the bird communities in January and February were likely even less diverse than in December and March. Bird abundance peaked during October in the autumn migration season (Ueuma 1979). Mt Takasaburo includes high montane areas of Japanese cool-temperate forests, whereas the OFR (620–680m) represents the low-montane forests of this type (Chapter 3). Thus, the general seasonal pattern of bird species diversity in Japanese cool-temperate deciduous forests entails an increase during breeding season, relatively high diversity being maintained during the autumn migration season, and a decline during winter, all with various magnitudes possibly depending on the severity of winter weather. Differences in tree composition between deciduous forests in the eastern (Pacific Ocean) side and in the western (Sea of Japan) side of the main range of Japan (Nakashizuka 2002) might have effects on the pattern.

The seasonal pattern of bird species diversity is primarily determined by climate, therefore different patterns may be expected in other natural forest types. In a subarctic mixed forest (43°44' N, 142°38' E) in central Hokkaido, the northernmost main island of Japan, seasonal pattern in both species richness and abundance showed steep convex curves that peak during the breeding season, because of the abundance of summer visitors there, whereas it was very low during both autumn and winter due to the small number of winter visitors and transients

(Fujimaki 1970). The seasonality of species richness in Bibai City (43°17' N, 141°52' E) in central Hokkaido also shows a similar pattern (Fujimaki 1973), although the study site includes various habitats. Thus, mixed forests are characterized by low autumn and winter bird diversity, possibly due to the harsher climate.

In a warm-temperate evergreen forest on Yakushima (Yaku Island, Kagoshima Prefecture; 30°20' N, 130°30' E, 1323 m a.s.l.) in southern Japan, the abundance of frugivorous birds was conversely high in winter and low in summer, with slightly higher species richness in winter than in summer for both frugivorous and other bird species (Noma and Yumoto 1997). In contrast, the seasonal pattern in a warm-temperate forest in central Japan (Boso Hills, Chiba Prefecture; 35°22' N, 140°11' E) showed fluctuating species richness without any clear seasonal trends (Karasawa 1971). Unlike the OFR, however, species richness was generally high in winter.

In a subtropical area, the bird species richness of a secondary forest at Tai Po Kau, Hong Kong (22°20' N, 114°11' E), was at its maximum in winter and at its minimum in summer, which reflects the much larger proportion of winter visitors than summer visitors (Kwok and Corlett 1999). Unlike Japanese warm-temperate forests, winter visitors in Tai Po Kau include insectivorous flycatchers (e.g. Brown Flycatcher *Muscicapa dauurica* and Mugimaki Flycatcher *Ficedula mugimaki*) and leaf warblers (e.g. Pallas's Leaf Warbler *Phylloscopus proregulus* and Yellow-browed Leaf Warbler *P. inornatus*).

Comparisons of seasonality in bird diversity along the East Asian Flyway suggest that each forest type differs in usage by migrants. Subarctic mixed forests are not widely used by migrants during the non-breeding season, most likely because of the harsh climatic conditions. Conversely, migrants use warm-temperate forests during both autumn migration and winter seasons, because evergreen forests provide stable wintering habitats for birds. Subtropical and,

probably, tropical forests provide wintering habitat also for insectivorous species that cannot overwinter in warm-temperate forests. Many migrants use cool-temperate forests mainly during the autumn migration season; thus, it is suggested that Japanese cool-temperate forests are important stopover sites for migratory birds.

Stopover sites may provide essential refueling points, even if individual birds visit them only for days or weeks (Newton 2004), and can influence the demography of migrants (Newton 2006). Cool-temperate forests provide food, such as fruits and seed crops, for migrants in autumn, as illustrated by the studies of seed-dispersal by birds in the OFR (e.g., Masaki et al. 1994). Stopover ecology has less studied in East Asia than in Europe (Yong et al. 2015).

Cool-temperate forests may be suitable as wintering habitats. It is known that the abundance of wintering birds in deciduous forests is greatly affected by annual food production, especially seed or fruit crops (Newton 1967). In fact, annual fluctuations in the production of sound seeds of the main component tree species, such as birch and beech, have been observed in the OFR (Shibata and Tanaka 2002). Thus, in years with good crops of these seeds, granivorous birds may feed in deciduous woodlands throughout winter.

#### **2-4-2 Variability of the non-breeding bird community**

NMDS ordination underlined the stability of bird communities during the breeding season and its variability during the non-breeding season, even when the bird communities in these seasons are apparently similar in species richness and abundance. At least three reasons are responsible for this variability. First, unlike the breeding season when breeding birds are tied to their nesting sites (Newton 2008), birds can move freely during the non-breeding season in response to temporal environmental changes. Temporal changes in feeding conditions, such as snowfall that inhibits feeding on the ground and herbaceous layer, may cause bird movements, as suggested

in this study and elsewhere in Japan (Inoue and Hashizume 1990, Oka and Nakamura 1998). Second, the non-breeding season incorporates the autumn migration season when migratory birds increase local bird diversity in both species richness and abundance. Although birds also migrate in spring, autumn migration is larger in magnitude and longer duration than in spring (e.g., Bayly and Gómez 2011), as autumn migration includes newly borne yearlings. Because the timing of autumn migration differs by species, temporary arrival of these species characterizes the assemblages of birds. Third, non-breeding birds often move in flocks, giving higher variances to census data (Nilsson 1974, Yui 1977, Greenwood et al. 1993). Large flocks of single species, such as Bramblings *Fringilla montifringilla* (Kaneko 1981) or waxwings in this study, can strongly affect total bird abundance.

The observed stability of the breeding bird community guarantees robustness to the timing of a census during the season. Conversely, given the variability during the non-breeding season, it seems difficult to determine data representative of the season. If the aim of the research is to survey winter bird fauna with a minimum of effort, an acceptable choice might be collecting data in December, when autumn migration is over and the effects of a severe winter might not yet be obvious, as some studies have done (Inoue and Hashizume 1990, Eguchi et al. 1992, Yamaura et al. 2009). However, as my results have shown, even in December, wintering flocks may greatly affect bird diversity, especially in abundance, and the result should be interpreted to include those possibilities.

This study documented the seasonal pattern shown by a bird community in a cool-temperate deciduous forest and indicated the importance of this forest type as a stopover site for migrants. Further examination of seasonal patterns in various forest types along the migration route would clarify their usage by birds with various migrating status. This study also revealed the variability of a bird community during the non-breeding season, as well as the

methodological difficulty of collecting appropriate data in this season. However, given the importance of wintering and stopover sites for the conservation of migrants, the poor understanding of seasonality in East Asia is a problem to be solved without delay.

2-5 Figures and Tables

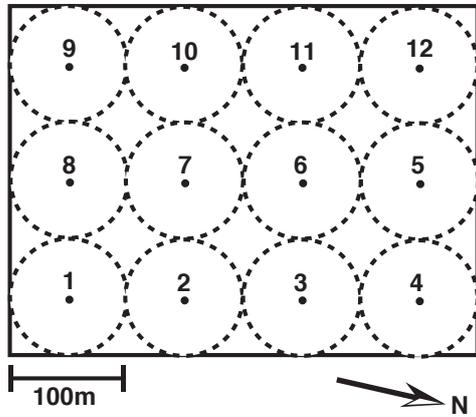


Fig. 2-1. Study plot for the Ogawa Forest Reserve bird survey. The outline square shows the 12-ha plot used for the survey using the territory mapping method (Chapter 3). Each circle indicates one survey area for the point count. Numbers in the circles denote the order of the census.

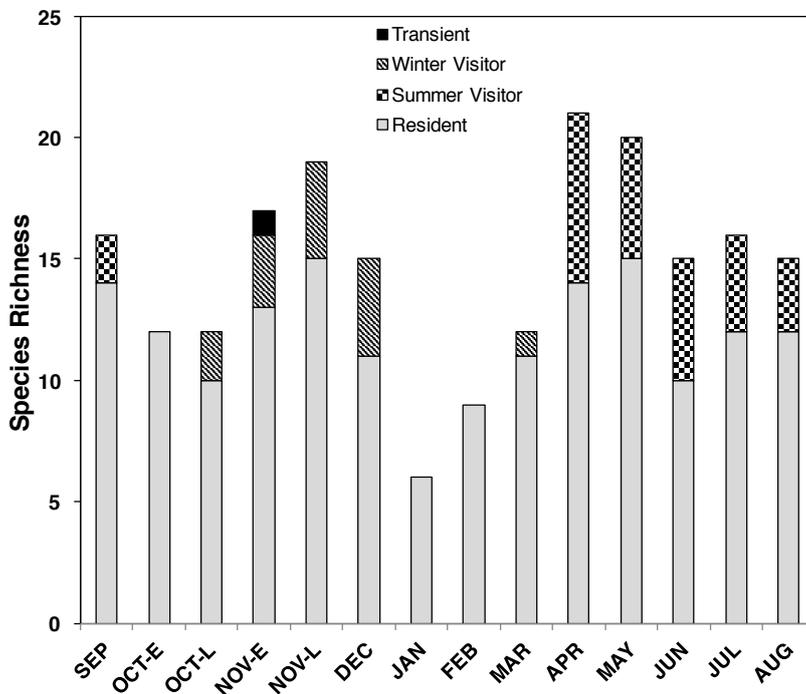


Fig. 2-2. Seasonal changes in bird species richness. Two censuses were conducted in early (E) and late (L) October and November.

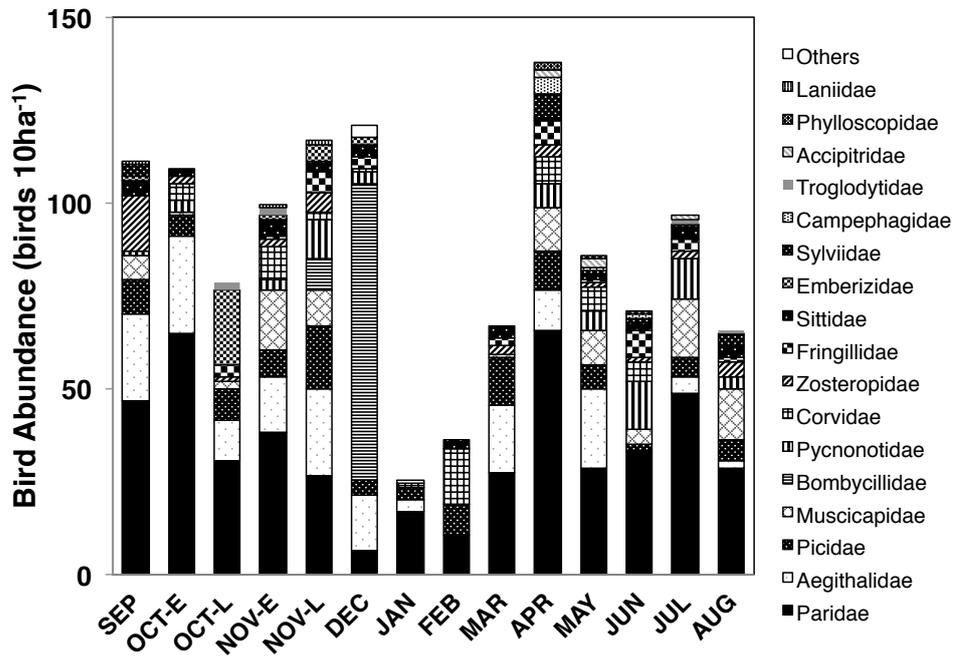


Fig. 2-3. Seasonal changes in bird abundance. Two censuses were conducted in early (E) and late (L) October and November.

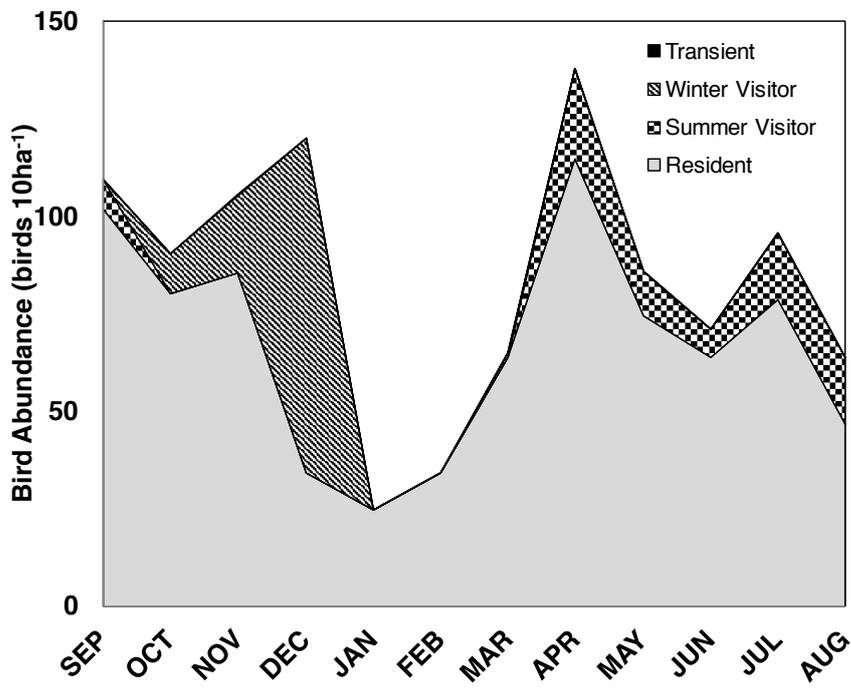


Fig. 2-4. Seasonal changes in bird abundance relative to migration status. Values in October and November were drawn from the averages of the two censuses.

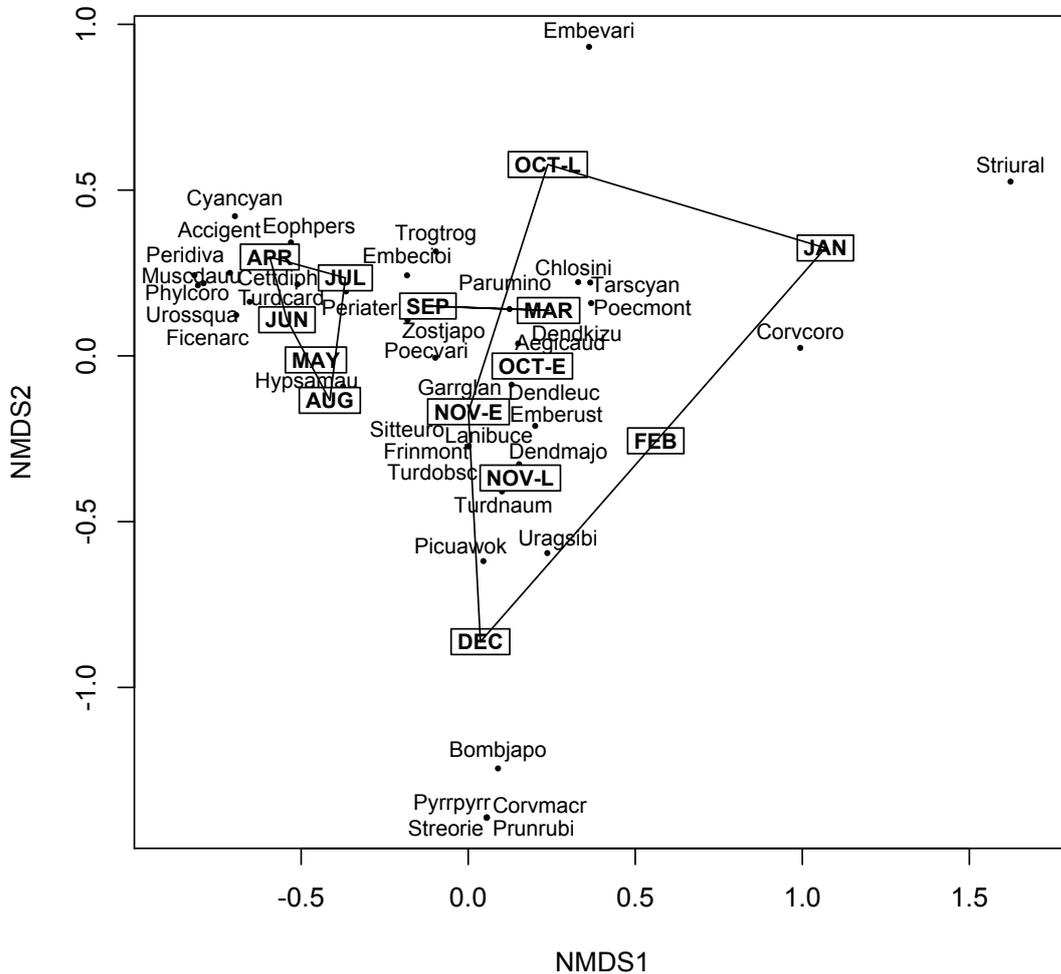


Fig. 2-5. An ordination using non-metric multidimensional scaling (NMDS). Stress value = 0.1386973. Months are grouped into breeding season (April–August), non-breeding season (October–February), and transition season (September and March). Variations in bird assemblage during the non-breeding season are greater than during the breeding season. Black dots indicate species positions with bird name labels reduced and arranged in order to minimize overlapping.

Table 2-1. Seasonality of the bird community in the OFR.

Family name	Common name	Scientific name	Status	SEP	OCT-E	OCT-L	NOV-E	NOV-L	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG
Phasianidae	Copper Pheasant	<i>Syrnaticus soemmerringii</i>	R										+				
Columbidae	Oriental Turtle Dove	<i>Streptopelia orientalis</i>	R						2								
Cuculidae	Rufous Hawk Cuckoo	<i>Hierococcyx hyperythrus</i>	SV													+	
	Lesser Cuckoo	<i>Cuculus poliocephalus</i>	SV												+	+	
	Oriental Cuckoo	<i>Cuculus optatus</i>	SV										+			+	
	Common Cuckoo	<i>Cuculus canorus</i>	SV												+	+	
Accipitridae	Black Kite	<i>Milvus migrans</i>	R									+					
	Northern Goshawk	<i>Accipiter gentilis</i>	R										2	2			1
Strigidae	Ural Owl	<i>Strix uralensis</i>	R							1							
Picidae	Japanese Pygmy Woodpecker	<i>Dendrocopos kizuki</i>	R	5	4	4	6	5	1	2	3	2	9	4	2	4	
	White-backed Woodpecker	<i>Dendrocopos leucotos</i>	R	1				4			2	7	1	1			2
	Great Spotted Woodpecker	<i>Dendrocopos major</i>	R		1		1	2	1		1	1		1			1
	Japanese Green Woodpecker	<i>Picus awokera</i>	R	1				2	1								
Campephagidae	Ashy Minivet	<i>Pericrocotus divaricatus</i>	SV										4	1	1		
Monarchidae	Japanese Paradise Flycatcher	<i>Terpsiphone atrocaudata</i>	SV													+	
Laniidae	Bull-headed Shrike	<i>Lanius bucephalus</i>	R	1			1	1									
Corvidae	Eurasian Jay	<i>Garrulus glandarius</i>	R		3		8	1			13		7	6	5		
	Carrion Crow	<i>Corvus corone</i>	R		1			1		1	1						
	Large-billed Crow	<i>Corvus macrorhynchos</i>	R						1								
Paridae	Willow Tit	<i>Poecile montanus</i>	R	10	19	17	4	5	3	10	3	3	3	4	3	2	3

Table 2-1. Seasonality of the bird community in the OFR. (Continued)

Family name	Common name	Scientific name	Status	SEP	OCT-E	OCT-L	NOV-E	NOV-L	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG
	Varied Tit	<i>Poecile varius</i>	R	11	7	3	8	5	2		6	4	10	2	9	12	15
	Coal Tit	<i>Periparus ater</i>	R	3	2	2	3					5	24	16	8	9	6
	Japanese Tit	<i>Parus minor</i>	R	20	33	7	21	15	1	6	1	14	25	5	11	23	3
Pycnonotidae	Brown-eared Bulbul	<i>Hypsipetes amaurotis</i>	R	1	3		3	10	3				6	5	12	10	3
Cettiidae	Japanese Bush Warbler	<i>Cettia diphone</i>	R	2									1	1			
	Asian Stubtail	<i>Urosphena squameiceps</i>	SV	1									5		1	1	3
Aegithalidae	Long-tailed Tit	<i>Aegithalos caudatus</i>	R	22	25	10	14	22	14	3		17	10	20		4	2
Phylloscopidae	Eastern Crowned Leaf Warbler	<i>Phylloscopus coronatus</i>	SV										2	1	1		
Zosteropidae	Japanese White-eye	<i>Zosterops japonicus</i>	R	14	2	1	2	5				2	3	1	1	2	4
Bombycillidae	Japanese Waxwing	<i>Bombycilla japonica</i>	WV					8	75								
Sittidae	Eurasian Nuthatch	<i>Sitta europaea</i>	R	4	2		4	3	3		2	3	1	1	2	3	3
Troglodytidae	Eurasian Wren	<i>Troglodytes troglodytes</i>	R			2	2									1	1
Muscicapidae	Scaly Thrush	<i>Zoothera dauma</i>	R														+
	Japanese Thrush	<i>Turdus cardis</i>	SV	6									3	2	2	8	8
	Eyebrowed Thrush	<i>Turdus obscurus</i>	T				1										
	Naumann's Thrush	<i>Turdus naumanni</i>	WV				12	9									
	Siberian Blue Robin	<i>Luscinia cyane</i>	SV														+
	Red-flanked Bluetail	<i>Tarsiger cyanurus</i>	WV									1					
	Daurian Redstart	<i>Phoenicurus auroreus</i>	WV							+							
	Asian Brown Flycatcher	<i>Muscicapa dauurica</i>	SV										3	2			

Table 2-1. Seasonality of the bird community in the OFR. (Continued)

Family name	Common name	Scientific name	Status	SEP	OCT-E	OCT-L	NOV-E	NOV-L	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG
	Narcissus Flycatcher	<i>Ficedula narcissina</i>	SV										4	5	2	6	5
	Blue-and-white Flycatcher	<i>Cyanoptila cyanomelana</i>	SV										1			1	
Prunellidae	Japanese Accentor	<i>Prunella rubida</i>	WV						1								
Fringillidae	Brambling	<i>Fringilla montifringilla</i>	WV				1										
	Oriental Greenfinch	<i>Chloris sinica</i>	R			1		3				2					
	Eurasian Siskin	<i>Carduelis spinus</i>	WV				+	+	+								
	Long-tailed Rosefinch	<i>Uragus sibiricus</i>	WV					2									
	Eurasian Bullfinch	<i>Pyrrhula pyrrhula</i>	WV						3								
	Japanese Grosbeak	<i>Eophona personata</i>	R			2							6	1	7	3	1
Emberizidae	Meadow Bunting	<i>Emberiza cioides</i>	R	1													
	Rustic Bunting	<i>Emberiza rustica</i>	WV			2	1	4	2								
	Grey Bunting	<i>Emberiza variabilis</i>	WV			17											
Total abundance				103	102	68	92	107	113	23	32	61	130	81	67	90	60
Species Richness				16	12	12	17	19	15	6	9	12	21	20	15	16	15

Sum of the counts from twelve 50m-radius circular plots (9.42 ha in total). + indicates the records outside the circular plots.

"-E" and "-L" indicate "early" and "late" of the month, respectively.

Status: R; parmanent residents, SV; summer visitor, WV; winter visitor, T; transient

## **Chapter 3 Breeding Bird Community of the Ogawa Forest Reserve**

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## **Chapter 3 Breeding Bird Community of the Ogawa Forest Reserve**

### **3-1 Introduction**

The preservation of biological diversity is one of the most important priorities of sustainable forest management. Birds are useful indicators of forest biodiversity, because they are diverse and sensitive to changes within the forest environment. A large number of species, however, is not necessarily the goal of forest management, because disturbances such as forest fragmentation often increase, rather than decrease, species diversity by creating habitat for generalists and edge-associated species (Tomiałojć and Wesołowski 1990, Lidicker et al. 1996, Kremsater and Bunnell 1999). In such cases, species vulnerable to those habitat changes may disappear, despite the increase in the total number of species. Thus, only those species present in the original, pristine vegetation type are relevant indicators of biodiversity (Opdam 1991). The documentation of avifauna in remnant old-growth forests is very important, because these species represent the original biodiversity of the ecosystem, thereby providing appropriate indicators for sustainable forest management.

In recent decades, Japanese primeval forests have been diminished and fragmented into small remnants due to human activities (Fukamachi et al. 1996). Even in the remaining forest reserves, the bird assemblages have likely changed. For example, recent declines of several tropical migrant bird species in Japan may be associated with habitat destruction in their over-wintering areas of Southeast Asia (Higuchi and Morishita 1999, Imanishi 2002). Additionally, several exotic birds, especially Timaliidae species, have recently invaded Japanese forests (Eguchi and Amano 2004) and have become dominant even in natural or old-growth

forests (Eguchi and Masuda 1994, Chapter 5). Thus, the examination and documentation of avifauna in Japanese primeval and old-growth forests are critical.

The patterns of the distribution of species can be determined on three spatial scales: habitat, landscape, and geography (Bestelmeyer et al. 2003). For primeval forests, biodiversity should be determined at the geographic level, because finer-scale variation due to human activities should be minimal. At the geographic level, both geographic location and elevation of sites may have significant effects on bird species diversity (e.g., Rahbek 1997, Shiu and Lee 2003). Given the steep Japanese topography, most regions of Japan contain a wide altitudinal gradient. Primeval or old-growth forests often remain only around mountain tops or on steep ridges, topographies unsuitable for plantation or development activities. In such cases, the elevations and the locations of primeval forests may differ markedly from those of other areas in the same region. Thus, to use data of a bird species diversity of a primeval forest as an indicator of sustainable forest management, it is necessary to determine what type of forest the diversity represents, by examining the effects of elevation and geographic location on it.

The Ogawa Forest Reserve (OFR; 98 ha; 36°56′ N, 140°35′ E) in Ibaraki Prefecture is a remnant old-growth deciduous forest dominated by deciduous trees, located in the southern part of the Abukuma Mountains in central Japan. Although regional differences among Japanese deciduous forests have been reported (e.g., Nakamura 1977, Yui 1977, Suzuki et al. 1991), the effects of geographic factors on them have not been discussed in detail. Here, the breeding bird community of the OFR was examined to estimate bird species diversity as the original bird fauna of the region. Then, the OFR avifauna was compared with those of other Japanese deciduous forests to clarify what type of forest it represented.

## **3-2 Materials and Methods**

### **3-2-1 Study site**

The OFR and surrounding areas have been subjected to human activities, such as burning, cattle grazing, and clear cutting for fuelwood, for at least the last 500 years (Nakashizuka 2002, Suzuki 2002). However, since the designation of the area as a forest reserve, the old-growth stands have been recovering and now closely resemble the original natural forest (Suzuki 2002). The OFR is rich in tree species, due in part to these previous large-scale disturbances; however, shade-intolerant species will eventually be eliminated in the future community (Masaki 2002).

### **3-2-2 Bird survey**

To examine bird diversity, I used the territory-mapping method (Williamson 1964), which estimates breeding territories by several surveys mapping territorial behavior. This method is particularly suitable for depicting the distribution of birds, although inefficient in terms of per unit fieldwork effort (Bibby et al. 2000). A 12-ha survey plot (400 × 300 m) was established, which included the 6-ha permanent plot used for the plant community study (Tanaka and Nakashizuka 2002). A stream passed through the center of the plot. No location within the survey plot was within 100 m of the forest edge; so edge effects on the bird community were minimal, if not negligible. A 50-m interval census route was established throughout the plot by setting marking flags.

Surveys were conducted from mid-April to mid-June 1994-1998. Ten census trips were conducted in each year. All signs of birds were registered on a map of the plot while walking the census route. The cumulative notations of a species during each year were used to determine territories. A territory that extended outside the plot was counted as 0.5 pair. The taxonomy and

nomenclature is based on the check-list of Japanese birds 6th revised edition (The Ornithological Society of Japan 2000).

### **3-2-3 Comparison to other Japanese deciduous forests**

Although a great deal of bird-census research has been conducted in Japan, most studies have used line-transect methods, whereas the territory-mapping method has been used in relatively few studies. Seven studies that used the territory mapping method were selected for deciduous stands (Table 3-1) from various locations in Honshu, the largest island of Japan (Fig. 3-1). With the exception of Hiruzen, all of the stands, including the OFR, had beech trees *Fagus* spp. as a dominant tree species (Table 3-1). The Hiruzen stand belongs to the “warm-temperate deciduous forest zone” (Inoue and Kondo 1983), a transition zone to evergreen forests. Ohdaigahara was the only plot that contained a coniferous tree species (*Picea jezoensis* var. *hondoensis*) as a dominant species (Hino 1990), and is considered to be in a transition zone to the sub-alpine zone. Consequently, stands with various locations and altitudes were included.

Most stands were primeval or old-growth forests, although a portion of the plot on Mt. Tsukuba was cut approximately 70 years ago, and in Hiruzen, clear-cut or grassland areas constituted 4.5% of the 20-ha plot (Inoue 1990). Inoue and Kondo (1983) did not describe the extent to which the plot was disturbed thoroughly. In Tayama, the bird density might have been underestimated, because the required number of census visits was not conducted (Yui 1983).

Species richness, abundance, annual stability, and species composition were compared among the stands. To investigate similarities in species composition among the stands, an unweighted pair-group method using arithmetic averages (UPGMA) cluster analysis of community composition was performed. Analyses were conducted using the program PC-ORD (McCune and Mefford 1999).

To examine differences in species composition among stands in relation to the geographic factors, I used ordination methods. As the length of the first axis drawn by a detrended correspondence analysis (DCA) was 2.41, the data are supposed to be linear context (ter Braak and Šmilauer 2002, Lepš and Šmilauer 2003). Then, I used a linear method, the principal component analysis (PCA). Then I fit the environmental vectors, the altitude, latitude, and longitude of each stand, onto the PCA ordination. The significances are calculated based on random permutation of the data. I used a software package R version 2.15.2 (R Development Core Team 2012) and R packages “vegan” for multivariate analysis of ecological communities (Oksanen 2013) and “MASS”.

The exotic Red-billed Leiothrix *Leiothrix lutea* was omitted to limit the comparison to native bird species. Although this species has become dominant on Mt. Tsukuba, the native avifauna has not yet been seriously affected by the invasion (Chapter 5). The Bush Warbler *Cettia diphone* was also omitted from the dataset used to compare species composition, because this species bred at high densities in dense understory regardless of forest type, which obscured the relationship between avifauna and forest type (Yui 1976, Hino 2000). Mean values were used from studies that included more than one census year (see Appendix 3-1).

### **3-3 Results**

#### **3-3-1 Bird assemblage of the OFR**

Sixty-three bird species were recorded during the study period (Table 3-2). Fifty-one out of the 63 species were potential breeders in the OFR, and the remaining 12 species were either remnant winter visitors or transient migrant species. Thirty-one out of the 51 species established territories during at least 1 of the 5 study years. The average number of breeding species and the average number of territories in the plot were 25.6 and 58.9, respectively (Table 3-2).

Twenty-one species occupied territories during all 5 census years (approximately 82% of the average number of breeding species). The coefficient of variance (CV) of the total number of territories for the 5 study years was 9.5%; therefore, the annual breeding community appeared stable. By contrast, five species, the Goshawk *Accipiter gentilis*, Japanese Green Pigeon *Sphenurus sieboldii*, Siberian Blue Robin *Luscinia cyane*, Brown Thrush *Turdus chrysolaus*, and Black Paradise Flycatcher *Terpsiphone atrocaudata*, established territories during only 1 year, although the plot size was too small to estimate the density of large species like the Goshawk.

The Great Tit *Parus major* was the most dominant species in the OFR and occupied an average of 12.2% of the total number of territories. Other dominant species included the Willow Tit *P. montanus*, Narcissus Flycatcher *Ficedula narcissina*, Coal Tit *P. ater*, Varied Tit *P. varius*, and Ashy Minivet *Pericrocotus divaricatus*, all of which occupied 6.1-7.0% of the total number of territories. Edge-associated species, such as the Siberian Meadow Bunting *Emberiza cioides* and Bull-headed Shrike *Lanius bucephalus*, did not establish territories in the plot, although they were common in the surrounding forest edges. The absence of these species indicated that the 12-ha plot was well inside the forest and likely experienced negligible edge effects (Lidicker et al. 1996, Kremsater and Bunnell 1999).

The breeding bird community of the OFR included many red-listed bird species designated in national and local red-data books. The red-data book of Japan (Ministry of the Environment Japan 2002) lists the Goshawk and Ashy Minivet as vulnerable species and the Japanese Night Heron *Gorsachius goisagi* as a near-threatened species. The local red-data book of Ibaraki Prefecture (Ibaraki Prefecture 2000) lists the Japanese Night Heron as endangered, the Goshawk and Japanese Robin *Erithacus akahige* as vulnerable, and an additional eleven species as rare (Table 3-2).

### **3-3-2 Comparison to other Japanese deciduous forests**

The species richness of other Japanese deciduous forests ranged from 14.8 to 32 species (Fig. 3-2 a). The species richness of the OFR was near the middle of the range. The abundance of the breeding birds in other Japanese deciduous forests was between 330 and 770 pairs per 100 ha, except for Tayama, where the survey effort was small (Fig. 3-2 b). Again, the bird abundance of the OFR was similar to the average of the other deciduous forests. Thus, in terms of species richness and abundance, the breeding bird community of the OFR is similar to other Japanese deciduous forests. The observed annual stability of the OFR bird community was also found to be similar to other Japanese deciduous forests. The CV of Tayama (Yui 1983) and Ohdaigahara (Hino 2000) during five study years, the same as this study, were also small (9.9 and 2.7 %, respectively).

In the cluster analysis, Kayanodaira and Ohdaigahara, the two high montane deciduous forests (>1400 m), exhibited a low level of similarity to other stands and to each other (Fig. 3-3). The remaining six stands were divided into two groups, which differed in the elevation of the stands (800-1400 m and <800 m). The OFR and two other low-montane stands, Mt. Tsukuba and Hiruzen, comprised the low-montane group. Thus, the species composition of deciduous forests seemed to be more closely related to the elevation than to the geographic location of the sites.

The PCA ordination separated the plots along axis 1 (Fig. 3-4). Kayanodaira had the highest score along axis 1, followed by Ohdaigahara. The OFR was plotted near Hiruzen with Mt. Tsukuba along axis 1 and the three stands had the lowest axis 1 scores among the plots. Eigenvalues of the first two axes and their cumulative percentage variance explained were, 7073.3, 1448.9, and 74.0 %, respectively.

Among the geographic variables for the stands, only altitude was significant correlation with the ordination (999 permutations). The latitudes and longitudes of the stands had little correlation with the ordination ( $r = 0.1367$ , NS and  $r = 0.2484$ , NS, 999 permutations, respectively) (Fig. 3-4). These results indicated that elevation had strong effects on the variation of the breeding bird assemblages of the stands compared.

### **3-4 Discussion**

#### **3-4-1 Status of bird species diversity in the OFR**

The species richness and abundance of the breeding bird community in the OFR were comparable to other mature deciduous forests of Honshu. Hino (1990) suggested that species richness and the abundance of Japanese mature deciduous forests were 25-35 species and 500 pairs per 100ha, respectively, and these are close to the values observed for the OFR. The observed annual stability of the breeding bird abundance of the OFR was also similar to other mature forests. Yui (1983) found that in mature or natural forests, the CV of the total number of territories in each plot remained close to 10%, which is similar to the value of 9.5% observed in the OFR.

The species composition also indicates the maturity of the bird assemblage of the OFR. Of the 51 potential breeders in the OFR, 14 species (27 %) are listed in national or local red-data books (Table 3-2). Considering recent declines in tropical migrant bird species in Japan (Higuchi and Morishita 1999, Amano and Yamaura 2007), the dominant status of the Ashy Minivet and Brown Flycatcher *Muscicapa dauurica* in the OFR seems particularly noteworthy. In addition to the destruction of tropical forests in their over-wintering area, habitat loss and fragmentation in the breeding area could cause declines of tropical migrants through increased risks of nest predation and brood parasites (e.g., Terborgh 1989, Askins et al. 1990, Paton 1994,

Robinson et al. 1995, Newton 2004). Heterogeneity in the rates of decline of tropical migrant species between breeding areas would support the latter hypothesis. Thus, the observed dominant status of the declining tropical migrants suggests that the OFR still provides a good breeding habitat for them, although the impacts of forest fragmentation on tropical migrants has not been confirmed in Japan (Kurosawa and Askins 1999, Askins et al. 2000, Kurosawa and Askins 2003).

The diverse woodpecker species of the OFR may prove the mature forest status of the OFR. The OFR had all four species of woodpeckers found in this region. Of these, the White-backed Woodpecker *Dendrocopos leucotos* is a mature-forest breeder and listed in the local red-data book as a “rare species” (Ibaraki Prefecture 2000). The old-growth vegetation of the OFR with many snags seems to be suitable for supporting the various woodpecker species (Matsuoka and Takada 1999), as well as other mature-forest birds. In Poland, the woodpecker species richness and the presence of the White-backed Woodpecker were good predictors of the species richness of other forest bird species, especially forest specialists (Mikusiński et al. 2001).

The species richness, abundance, annual stability, and species composition suggest that the breeding bird community of the OFR is similar to the original bird community. The OFR had been subjected to human disturbances for long periods and has currently reached the mature forest stage as a forest reserve (Nakashizuka and Matsumoto 2002). The OFR seems to have recovered the primeval bird community with the recovery of the vegetation, although some species might have been lost during the past disturbances. Thus, the OFR provides an example of the original bird diversity of the region.

### **3-4-2 What type of forest does the OFR represent?**

The cluster and ordination analyses of the bird assemblages in Japanese deciduous forests indicate the importance of the elevation gradient in determining species composition. In Japan, the bird species turnover along elevation gradients has been documented in regions containing more than one forest type (e.g., Kiyosu 1966, Hino 1993). The results here underline that even within the restricted altitudinal range of the deciduous forest zone in Honshu (ca. 600-1500 m; Table 1), the elevation still strongly affects the species composition of bird assemblages. Thus, the bird assemblage of the OFR can be characterized as representing low-montane deciduous forest.

In contrast, the bird assemblage of the OFR could not be characterized by geographic location. If the comparisons included the northernmost Japanese deciduous forests of Hokkaido and the southernmost ones of Kyushu, geographic location would have had more effect on the bird species composition (e.g., Suzuki et al. 1991). Among the deciduous forests of Honshu, however, geographic location had only small effects on it. This indicates that the bird assemblage of the OFR represents not only the original deciduous forests of central Japan, but also the low-montane deciduous forests of most regions of Honshu.

The lowland areas of Japan have often been severely affected by human activities. The abandonment and loss of the traditional landscapes (“*Satoyama*”) in recent decades are partly responsible for the current biodiversity crisis in low-montane areas of Japan (Washitani 2001, Takeuchi et al. 2003). This study has shown that the OFR represents the original avifauna in a *Satoyama* area, and it may also represent the original bird species diversity of low-montane deciduous forest areas of Honshu. The representation of the original bird diversity of these areas will be an important indicator for evaluating the sustainability of forest management.

Considering the vulnerability of these low-montane areas, the avifauna of the OFR is valuable and should be preserved and monitored carefully.

### 3-5 Figures and Tables

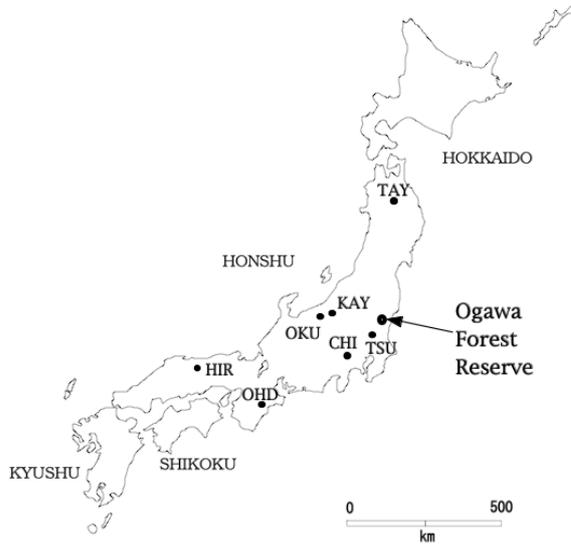


Fig. 3-1. Location of the Ogawa Forest Reserve (OFR) and other forest stands examined in this survey. See Table 3-1 for abbreviations.

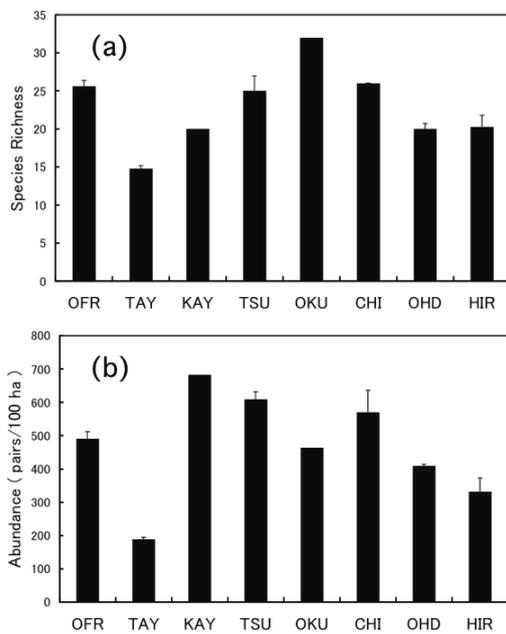


Fig. 3-2. Species richness (a) and abundance (b) of Japanese deciduous forests. Error bars show SE.

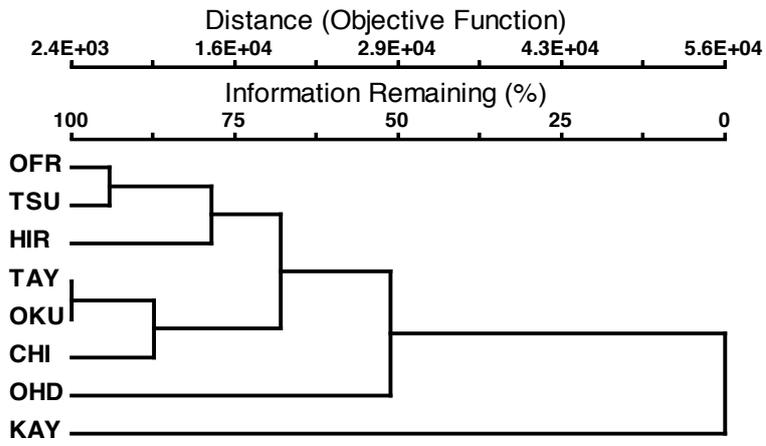


Fig. 3-3. Dendrogram resulting from the UPGMA cluster analysis of eight bird assemblages of Japanese deciduous forests. See Table 3-1 for abbreviations.

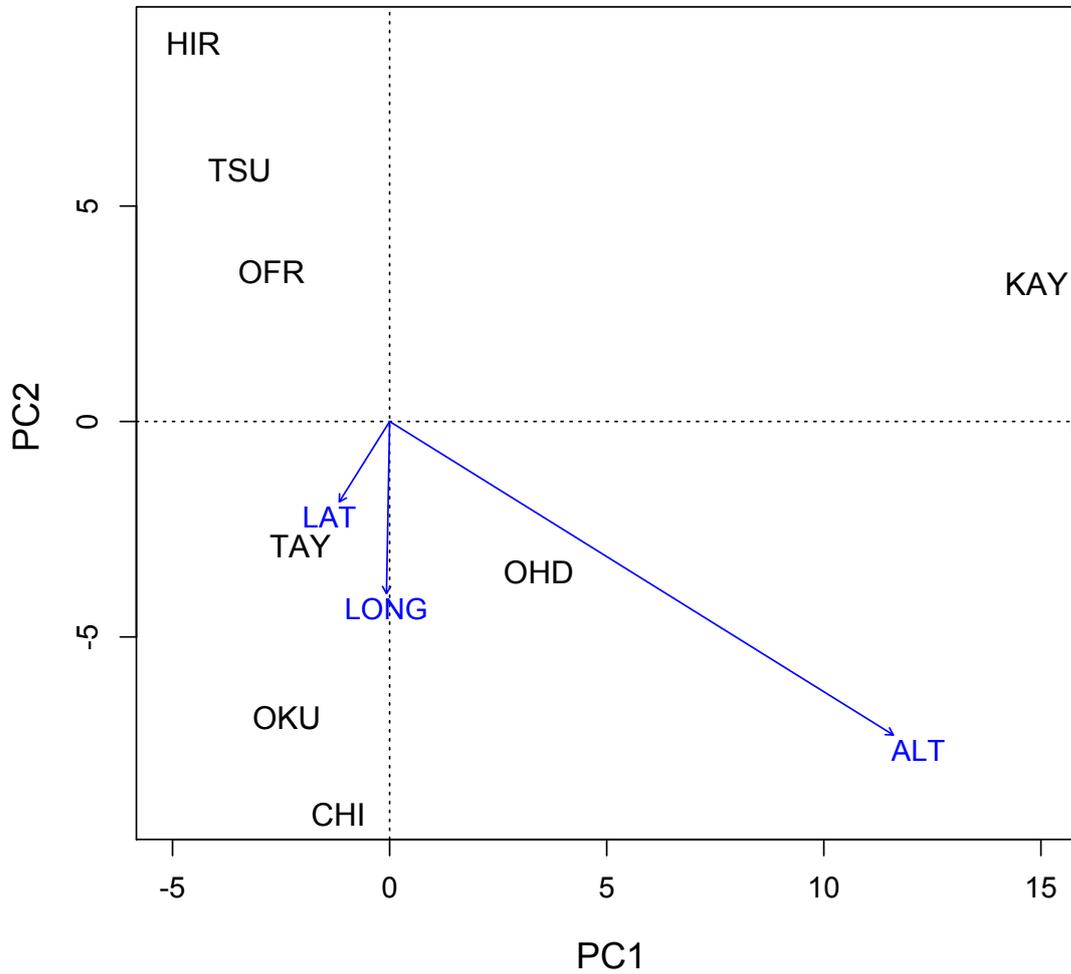


Fig. 3-4. Ordination diagram from the principal component analysis (PCA) of eight bird assemblages. The angle and length of lines indicate the direction and strength of the relationships, respectively, between the ordination axes and the three geographic variables, ALT: altitude, LAT: latitude, LONG: longitude. See Table 3-1 for abbreviations.

Table 3-1. Breeding bird surveys using territory-mapping methods in Japanese deciduous forests

Source	Site name	Abbreviation	Plot size	Study years	Latitude(N)	Longitude(E)	Altitude(m)	Dominant tree species
Present study	Ogawa Forest Reserve	OFR	12 ha	5	36.9	140.6	620-680	<i>Quercus serrata</i> , <i>Q. crispula</i> , <i>Fagus japonica</i> , <i>F. crenata</i>
Yui 1983	Tayama	TAY	13 ha	5	40.1	140.9	800	<i>Fagus crenata</i>
Nakamura 1986	Kayanodaira	KAY	5.7 ha	1	36.8	138.5	1460-1500	<i>Fagus crenata</i>
Chapter 5	Mt. Tsukuba	TSU	8 ha	2	36.2	140.1	700-800	<i>Fagus crenata</i> , <i>Quercus crispula</i> , <i>Prunus jamasakura</i>
Mitsuishi 1970	Okususobana	OKU	2986 m*	1	36.8	138.0	1200-1400	<i>Fagus crenata</i>
Uramoto 1961	Chichibu-Tama	CHI	2750 m*	2	35.9	139.0	900-1200	<i>Fagus crenata</i> , <i>F. japonicas</i>
Hino 2000	Ohdaigahara	OHD	12ha	5	34.2	136.1	1550	<i>Fagus crenata</i> , <i>Picea jezoensis</i> , <i>Acer shirasawanum</i>
Inoue 1990	Hiruzen	HIR	20 ha	4	35.3	133.6	690-780	<i>Quercus serrata</i> , <i>Q. acutissima</i>

\* Territories were mapped along a census belt with width determined for each bird species.

Table 3-2. Number of breeding-bird territories in a 12-ha plot in the Ogawa Forest Reserve

Family name	Common name	Scientific name	Threat	Status	1994	1995	1996	1997	1998	average	%
Ardeidae	Japanese Night Heron	<i>Gorsachius goisagi</i>	NT,e	TM	+					+	
Anatidae	Mandarin Duck	<i>Aix galericulata</i>	r	R			+			+	
Accipitridae	Black Kite	<i>Milvus migrans</i>		R	+	+	+	+		+	
	Goshawk	<i>Accipiter gentilis</i>	VU,v	R				0.5		0.1	0.2
	Buzzard	<i>Buteo buteo</i>		R	+	+	+	+	+	+	
	Grey-faced Buzzard-eagle	<i>Butastur indicus</i>		TM		+				+	
Phasianidae	Chinese Bamboo Partridge	<i>Bambusicola thoracica</i>		R		+				+	
	Copper Pheasant	<i>Syrmaticus soemmerringii</i>		R	+	+	+	+	+	+	
Columbidae	Rufous Turtle Dove	<i>Streptopelia orientalis</i>		R	1	1.0	1.0	0.5	1.0	0.9	1.5
	Japanese Green Pigeon	<i>Sphenurus sieboldii</i>		R	+	0.5	+		+	0.1	0.2
Cuculidae	Fugitive Hawk Cuckoo	<i>Cuculus fugax</i>	r	TM	+					+	
	Common Cuckoo	<i>Cuculus canorus</i>	r	TM	+	+	+		+	+	
	Oriental Cuckoo	<i>Cuculus saturatus</i>		TM	+	0.5	1.0	0.5	0.5	0.5	0.8
	Little Cuckoo	<i>Cuculus poliocephalus</i>		TM	+	+	+	+	+	+	
Strigidae	Ural Owl	<i>Strix uralensis</i>		R		+	+		+	+	
Caprimulgidae	Jungle Nightjar	<i>Caprimulgus indicus</i>		TM		+				+	
Picidae	Japanese Green Woodpecker	<i>Picus awokera</i>		R	1	1.0	1.0	1.0	1.0	1.0	1.7
	Great Spotted Woodpecker	<i>Dendrocopos major</i>		R	+	1.5	1.0	1.0	1.5	1.0	1.7
	White-backed Woodpecker	<i>Dendrocopos leucotos</i>	r	R	1.5	1.5	1.0	1.0	1.0	1.2	2.0
	Japanese Pygmy Woodpecker	<i>Dendrocopos kizuki</i>		R	3	2.5	3.5	3.5	3.0	3.1	5.3
Motacillidae	Grey Wagtail	<i>Motacilla cinerea</i>		R	+	+	+	+	+	+	
	Olive-backed Pipit	<i>Anthus hodgsoni</i>		W					+	+	

Table 3-2. Number of breeding-bird territories in a 12-ha plot in the Ogawa Forest Reserve. (Continued)

Family name	Common name	Scientific name	Threat	Status	1994	1995	1996	1997	1998	average	%
Campephagidae	Ashy Minivet	<i>Pericrocotus divaricatus</i>	VU,r	TM	3	3.5	4.0	3.5	4.0	3.6	6.1
Pycnonotidae	Brown-eared Bulbul	<i>Hypsipetes amaurotis</i>		R	2.5	3.0	3.0	3.0	3.0	2.9	4.9
Bombycillidae	Japanese Waxwing	<i>Bombycilla japonica</i>		W					+	+	
Troglodytidae	Winter Wren	<i>Troglodytes troglodytes</i>		R	1	0.5	0.5	+	0.5	0.5	0.8
Turdidae	Japanese Robin	<i>Erithacus akahige</i>	v	TM				+		+	
	Siberian Blue Robin	<i>Luscinia cyane</i>	r	TM		+		0.5	+	0.1	0.2
	White's Thrush	<i>Zoothera dauma</i>		R	1	0.5	0.5		+	0.4	0.7
	Siberian Thrush	<i>Turdus sibiricus</i>	r	TM	+	+				+	
	Grey Thrush	<i>Turdus cardis</i>		TM	2.5	2.0	2.0	2.5	2.5	2.3	3.9
	Brown Thrush	<i>Turdus chrysolaus</i>		SM			0.5			0.1	0.2
	Pale Thrush	<i>Turdus pallidus</i>		W		+	+	+		+	
Sylviidae	Dusky Thrush	<i>Turdus naumani</i>		W	+		+			+	
	Short-tailed Bush Warbler	<i>Urosphena squameiceps</i>		TM	1.5	2.0	0.5	2.5	3.0	1.9	3.2
	Bush Warbler	<i>Cettia diphone</i>		R	1.5	1.0	1.0	1.0	1.0	1.1	1.9
	Arctic Warbler	<i>Phylloscopus borealis</i>		T			+			+	
	Eastern Pale-legged Leaf Warbler	<i>Phylloscopus borealoides</i>		T					+	+	
Muscicapidae	Eastern Crowned Leaf Warbler	<i>Phylloscopus coronatus</i>		TM	1	1.5	1.0	2.0	3.0	1.7	2.9
	Narcissus Flycatcher	<i>Ficedula narcissina</i>		TM	3	4.5	4.0	4.5	4.0	4.0	6.8
	Blue and White Flycatcher	<i>Cyanoptila cyanomelana</i>	r	TM		1.5	+	2.0	1.0	0.9	1.5
Monarchidae	Brown Flycatcher	<i>Muscicapa dauurica</i>	r	TM	2.5	2.5	2.0	3.0	3.5	2.7	4.6
	Black Paradise Flycatcher	<i>Terpsiphone atrocaudata</i>	r	TM	+	+	0.5			0.1	0.2
Aegithalidae	Long-tailed Tit	<i>Aegithalos caudatus</i>		R	2.5	3.0	3.0	4.5	2.0	3.0	5.1
Paridae	Willow Tit	<i>Parus montanus</i>		R	3.5	4.0	4.5	4.0	4.5	4.1	7.0

Table 3-2. Number of breeding-bird territories in a 12-ha plot in the Ogawa Forest Reserve. (Continued)

Family name	Common name	Scientific name	Threat	Status	1994	1995	1996	1997	1998	average	%
	Coal Tit	<i>Parus ater</i>		R	3	3.5	4.5	5.5	3.5	4.0	6.8
	Varied Tit	<i>Parus varius</i>		R	2.5	3.5	3.0	4.5	4.5	3.6	6.1
	Great Tit	<i>Parus major</i>		R	7	6.5	7.5	7.5	7.5	7.2	12.2
Sittidae	Nuthatch	<i>Sitta europaea</i>	r	R	1	1.5	2.0	2.0	2.5	1.8	3.1
Zosteropidae	Japanese White-eye	<i>Zosterops japonicus</i>		R	3	1.5	2.5	2.0	3.5	2.5	4.2
Emberizidae	Siberian Meadow Bunting	<i>Emberiza cioides</i>		R		+	+		+	+	
	Rustic Bunting	<i>Emberiza rustica</i>		W	+		+		+	+	
	Black-faced Bunting	<i>Emberiza spodocephala</i>		W	+		+	+	+	+	
	Gray Bunting	<i>Emberiza variabilis</i>		W	+	+	+	+		+	
Fringillidae	Brambling	<i>Fringilla montifringilla</i>		W	+					+	
	Oriental Greenfinch	<i>Carduelis sinica</i>		R	+		+		+	+	
	Siskin	<i>Carduelis spinus</i>		W					+	+	
	Bullfinch	<i>Pyrrhula pyrrhula</i>		W		+		+	+	+	
	Japanese Grosbeak	<i>Eophona personata</i>		R	1.5	0.5	1.0	1.0	1.0	1.0	1.7
	Hawfinch	<i>Coccothraustes coccothraustes</i>		W	+	+	+			+	
Corvidae	Jay	<i>Garrulus glandarius</i>		R	1.5	1.5	1.5	1.5	1.5	1.5	2.5
	Carrion Crow	<i>Corvus corone</i>		R			+	+		+	
	Jungle Crow	<i>Corvus macrorhynchos</i>		R	+	+	+	+	+	+	
Total number of territories					51.5	56.5	57.5	65.0	64.0	58.9	100
Number of species with territories						23	27	27	26	25	25.6

Status: Status in the OFR, TM; tropical migrant, SM; short-distant migrant, R; permanent resident, W; winter visitor, T; transient.

Threat: capitals; National Red-list (Ministry of the Environment of Japan 2002), V; vulnerable, NT; near threatened;

small letters; Local Red-list (Ibaraki Prefecture 2000), e; endangered, v; vulnerable, r; rare. + : Presence in the plot without occupying territories.

Appendix 3-1. Density of breeding birds (pairs/100 ha) in breeding bird surveys in Japanese deciduous forests.

Family	Common name	Scientific name	OFR	TAY	KAY	TSU	OKU	CHI	OHD	HIR
Accipitridae	Goshawk	<i>Accipiter gentilis</i>	0.8							
Phasianidae	Copper Pheasant	<i>Syrmaticus soemmerringii</i>				6.3	4.2	9.0	4.2	6.9
Columbidae	Rufous Turtle Dove	<i>Streptopelia orientalis</i>	7.5			6.3	6.7			1.3
	Japanese Green Pigeon	<i>Sphenurus sieboldii</i>	0.8					3.0		5.6
Cuculidae	Fugitive Hawk Cuckoo	<i>Cuculus fugax</i>		3.1		6.3			4.2	
	Common Cuckoo	<i>Cuculus canorus</i>			7.0		4.8			
	Oriental Cuckoo	<i>Cuculus saturatus</i>	4.2	1.5	2.0	12.5	4.8		4.2	
	Little Cuckoo	<i>Cuculus poliocephalus</i>			5.5	18.8	7.2			6.9
Caprimulgidae	Jungle Nightjar	<i>Caprimulgus indicus</i>					3.4			
Alcedinidae	Greater Pied Kingfisher	<i>Ceryle lugubris</i>								1.3
	Ruddy Kingfisher	<i>Halcyon coromanda</i>					2.4			
Picidae	Japanese Green Woodpecker	<i>Picus awokera</i>	8.3			12.5		4.0	1.7	9.4
	Great Spotted Woodpecker	<i>Dendrocopos major</i>	8.3	3.8	10.5		7.2	4.0	8.3	4.4
	White-backed Woodpecker	<i>Dendrocopos leucotos</i>	10.0	4.6				4.0	8.3	1.3
	Japanese Pygmy Woodpecker	<i>Dendrocopos kizuki</i>	25.8	1.5	1.5	31.3	25.1	25.0	20.8	18.1
Motacillidae	Grey Wagtail	<i>Motacilla cinerea</i>					10.1			
	Olive-backed Pipit	<i>Anthus hodgsoni</i>			7.0				0.8	
Campephagidae	Ashy Minivet	<i>Pericrocotus divaricatus</i>	30.0				3.4			4.4
Pycnonotidae	Brown-eared Bulbul	<i>Hypsipetes amaurotis</i>	24.2			18.8				47.5
Laniidae	Bull-headed Shrike	<i>Lanius bucephalus</i>			12.5		3.4			5.6
Troglodytidae	Winter Wren	<i>Troglodytes troglodytes</i>	4.2			12.5	23.4	23.0	35.0	

Appendix 3-1. Density of breeding birds (pairs/100 ha) in breeding bird surveys in Japanese deciduous forests. (Continued)

Family	Common name	Scientific name	OFR	TAY	KAY	TSU	OKU	CHI	OHD	HIR
Trudidae	Japanese Robin	<i>Erithacus akahige</i>				6.3	3.0	1.5	8.3	
Trudidae	Siberian Blue Robin	<i>Luscinia cyane</i>	0.8	20.0	35.0	18.8	41.2	72.0		
	Red-flanked Bushrobin	<i>Tarsiger cyanurus</i>							33.3	
	White's Thrush	<i>Zoothera dauma</i>	3.3				2.4	4.0		3.1
	Siberian Thrush	<i>Turdus sibiricus</i>		1.5			12.0	5.0		
	Grey Thrush	<i>Turdus cardis</i>	19.2			6.3	2.4			6.3
	Brown Thrush	<i>Turdus chrysolaus</i>	0.8	1.5	5.5			5.0	8.3	
Sylviidae	Short-tailed Bush Warbler	<i>Urosphena squameiceps</i>	15.8	4.6		43.8		38.5		3.8
	Bush Warbler	<i>Cettia diphone</i>	9.2		14.0	131.3	22.3	40.0		41.3
	Arctic Warbler	<i>Phylloscopus borealis</i>							10.0	
	Eastern Pale-legged Leaf Warbler	<i>Phylloscopus borealoides</i>		10.8			3.4	13.0	1.7	
	Eastern Crowned Leaf Warbler	<i>Phylloscopus coronatus</i>	14.2	4.6		12.5	33.5	45.0		
Muscicapidae	Narcissus Flycatcher	<i>Ficedula narcissina</i>	33.3	30.0	3.5	18.8	45.5	36.0		
	Blue and White Flycatcher	<i>Cyanoptila cyanomelana</i>	7.5			12.5	11.2	8.0	8.3	0.6
	Sooty Flycatcher	<i>Muscicapa sibirica</i>					8.4		1.7	
	Brown Flycatcher	<i>Muscicapa dauurica</i>	22.5					7.0		
Monarchidae	Black Paradise Flycatcher	<i>Terpsiphone atrocaudata</i>	0.8							
Aegithalidae	Long-tailed Tit	<i>Aegithalos caudatus</i>	25.0	2.3		37.5		23.5	1.7	10.6
Paridae	Willow Tit	<i>Parus montanus</i>	34.2	13.8	26.5	18.8	16.7	29.0	5.0	14.4
	Coal Tit	<i>Parus ater</i>	33.3	33.1	210.5	18.8	30.4	55.5	118.3	
	Varied Tit	<i>Parus varius</i>	30.0	2.3		31.3	13.4	29.0	26.7	14.4
	Great Tit	<i>Parus major</i>	60.0	19.2	87.5	93.8	50.2	49.0	39.9	39.4

Appendix 3-1. Density of breeding birds (pairs/100 ha) in breeding bird surveys in Japanese deciduous forests. (Continued)

Family	Common name	Scientific name	OFR	TAY	KAY	TSU	OKU	CHI	OHD	HIR
Sittidae	Nuthach	<i>Sitta europaea</i>	15.0	19.2	9.0		36.1	20.5	33.3	7.5
Certhiidae	Tree Creeper	<i>Certhia familiaris</i>							16.6	
Zosteropidae	Japanese White-eye	<i>Zosterops japonicus</i>	20.8			37.5				7.5
Emberizidae	Siberian Meadow Bunting	<i>Emberiza cioides</i>			7.0	12.5	3.4			44.4
	Grey Bunting	<i>Emberiza variabilis</i>			63.0					
Fringillidae	Japanese Grosbeak	<i>Eophona personata</i>	8.3		17.5	6.3				14.4
Ploceidae	Russet Sparrow	<i>Passer rutilans</i>			87.5					
Sturnidae	Red-cheeked Myna	<i>Sturnus philippensis</i>			70.0					
Corvidae	Jay	<i>Garrulus glandarius</i>	12.5	11.5		12.5	20.1	16.5	8.3	11.9
	Carrion Crow	<i>Corvus corone</i>					2.4			
Timaliidae	Red-billed Leiothrix	<i>Leiothrix lutea</i>				418.8				
Total density			490.8	189.2	682.5	1062.5	464.1	570.0	408.9	332.2
Total number of species			31	19	20	27	32	26	24	26

Bush Warbler and Red-billed Leiothrix were eliminated from comparison. See text.

## **Chapter 4 Effects of Stand Type and Age on Bird Species Diversity in Central Japan**

The contents of this chapter are not disclosed because the materials to be scheduled for submission to academic journals.

## **Chapter 5 Breeding Density of Exotic Red-billed Leiothrix and Native Bird Species on Mt. Tsukuba, Central Japan**

The contents of this chapter have been published in:

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Leiothrix and native bird species on Mt. Tsukuba, central Japan.

Ornithological Science 3, p.23-32.

## **Chapter 5 Breeding Density of Exotic Red-billed Leiothrix and Native Bird Species on Mt. Tsukuba, Central Japan**

### **5-1 Introduction**

The Red-billed Leiothrix *Leiothrix lutea* is native to Himalayas, Assam, western and northern Myanmar, southern China and northern Vietnam (MacKinnon and Phillipps 2000). This species is a popular cage bird and has been introduced successfully into the Hawaiian Islands (Berger 1981, Long 1981, Ralph et al. 1998). Around 1980, breeding populations of leiothrix were found in the southern, western and central parts of Japan and have increased in numbers since then (Eguchi and Masuda 1994, Tojo 1994).

Although many exotic bird species have naturalized in Japan (Ecological Society of Japan 2002), most of them breed exclusively in man-modified habitats. The sole exotic species that invaded Japanese forests by 1970's is the Chinese Bamboo Partridge *Bambusicola thoracica*. This partridge was introduced and released in 1919 and became established in warm temperate areas in Japan (Kiyosu 1978), although its main habitats are dense bushes and cultivated fields, not large forest tracts nor deep mountains. The preferences for man-modified habitats in exotic species are also seen in other countries and islands. Diamond and Veitch (1981) explored New Zealand avifaunas and concluded that only after decimation of native species and forest alteration by browsing mammals could exotic birds invade forests. On the other hand, Case (1996) examined the global patterns in the establishment and distribution of exotic birds and found that the most important correlates of success of exotic birds is the number of native species extinctions, which reflects the degree of human activity and habitat destruction and deterioration through the introduction of exotic predators, herbivores and parasites.

Unlike earlier avian invaders in Japan, main breeding habitats of leiothrix are natural deciduous forests. In Kyushu, it breeds in deciduous forests as well as *Tsuga* and *Abies* forests with dense undergrowth above 1000 m in elevation and became the most dominant species in some areas (Eguchi and Masuda 1994, Eguchi and Amano 2000). The successful invasion of leiothrix into Japanese deep forests seems to contradict the general trend and severe competition with native bird species of such natural forests may be expected. Mountainspring and Scott (1985) explored passerine birds associations in native forests in the Hawaiian Islands, which exotic Red-billed Leiothrix, Japanese White-eye *Zosteropus japonicus*, and Melodious Laughing Thrush *Garrulax canorus* have invaded, and found that native/exotic species-pairs had a significantly greater proportion of negative partial correlations than either native/native pairs or exotic/exotic pairs. They argued that although the negative correlations were for the most part small, one species could eventually replace another as spatial displacement accumulated through time.

Unfortunately, as monitoring data on avifauna of Japanese forests into which leiothrix have penetrated are not available in most cases, detection of its effects is difficult. However, when the invasion occurred in small, isolated ecosystems, serious effects, including competitive local exclusion, might occur, as Mountainspring and Scott (1985) expected. They also pointed out that if competition occurs between native and exotic species, it seems reasonable to expect it to be most severe during population explosions. Therefore, the rapid increase of leiothrix since 1980's might have caused drastic changes in certain native bird populations, a problem needing study.

In this paper, I research breeding density of the exotic Red-billed Leiothrix and native bird species in an isolated natural deciduous forest in order to document how leiothrix have increased in it. Then, I examine its effects on the native bird community by comparing my

census results with an avifaunal list on Mt. Tsukuba before leiothrix invasion and with bird communities of other similar Japanese forests.

## **5-2 Study Sites and Methods**

The study was performed in a deciduous forest on Mt. Tsukuba (877m, 36°13'N, 140°06'E), a major breeding area of leiothrix in central Japan. Although Mt. Tsukuba is not a high mountain, as it stands between warm-temperate and cool-temperate zone, its natural vegetation changes in relation to altitude, from broad-leaved evergreen forest in lowland area to broad-leaved deciduous forest around the summits. A deciduous forest, typical cool-temperate forest type in Japan, is the dominant vegetation above 700m alt. around the two peaks of Mt. Tsukuba. Smaller deciduous forests also occur at some lower summits within surrounding hill areas (Ibaraki Prefectural Forest Experiment Station 1980, Fukamachi et al. 1996).

While a part of the forest areas on Mt. Tsukuba has been protected by the Tsukuba Shrine and by the Japanese government, it also has been used for tourist industries and public institutions. Tourists can reach 800 m alt. by a cable tramcar or by a ropeway, and many constructions, such as tramcar stations, restaurants, souvenir shops, a climate observatory and an electric wave observatory, have been built between the two peaks. About half of them are concentrated in a small open area named "Miyukigahara". A part of the deciduous forest was cut about 70 years ago.

The first known record of leiothrix on Mt. Tsukuba was of three individuals in October 1980 (Ishii 1992). Leiothrix breeds in the deciduous forest around the peaks of Mt. Tsukuba in dense numbers, but probably wanders to lower areas in flocks during non-breeding season, as done in their native range (e.g., Ali 1977). A monthly bird census in a forest on a hillside (300 m alt.) 9 km apart from the main peaks of Mt. Tsukuba showed that leiothrix had increased in

number during 1988-1993 and 33 individuals were captured within 2 days in October 1992 (Tojo 1994).

Territory mapping method (Williamson 1964, Bibby et al. 1992) was used to estimate breeding density of birds of the deciduous forest. I set an 8 ha plot (east-west 400 m, south-north 200 m, about 700-800 m alt.) on the north slope of Mt. Tsukuba. Beech *Fagus crenata*, oak *Quercus crispula*, cherry *Prunus jamasakura* are the dominant canopy species. Thick understory growth of dwarf bamboo *Sasamorpha borealis*, which reach up to 200 cm, is found over most of area. A part of the southern edge of the plot is within 50 m from Miyukigahara and the northern edge is in contact with red pine *Pinus densiflora* stands and Japanese cedar *Cryptomeria japonica* plantations, which are located in lower areas of the northern slope on Mt. Tsukuba. A census route was made so as to come within 50 m of every point on the plot. Ten census trips were carried out from mid April to mid June in both 1994 and 1995. Territory that extended outside the plot was counted as 0.5 pair.

In 1995, I set a 1 ha intensive area within the 8 ha plot and tried to locate all leiothrix nests in it. As I had carried out a banding survey by mist netting, a number of the leiothrix were uniquely colour banded, which helped in identifying territory holders.

As far as I know, there is no quantitative data of avifauna on Mt. Tsukuba before leiothrix invasion, although Haga (1988) prepared a list of birds observed on Mt. Tsukuba during the previous ten years. This includes a period before the first record of leiothrix in 1980. The 76 species listed contains birds seen in the whole area of Mt. Tsukuba throughout the year. I excluded species that were not recorded in the breeding bird census by territory mapping in the deciduous forest on Mt. Tsukuba, such as raptors, nocturnal, aerial, aquatic and farmland species (see appendix for details). Breeding status of some short distant migrants on Mt. Tsukuba was difficult to judge. I excluded the Brown Thrush *Turdus chrysolaus* and the

Grey-faced Bunting *Emberiza spodocephala*, which might have bred during this period, as well as the Goldcrest *Regulus regulus*, that Haga (1988) described as a “winter visitor, but some records in summer”. A list of 35 species remained, that likely to be breeding birds before leiothrix invasion, are compared to our census results.

Another comparison is with similar Japanese forests. Hino (1990) reviewed avifaunal studies in Japanese mature deciduous forests and found that 25-35 species had territories and total densities were about 500 pairs per 100 ha. He selected four studies that satisfied following criteria: (1) mapping census methods had to be used; (2) forest age had to be at least 100 years; (3) coniferous trees were not a major component of the forests; and (4) the forest area, including census site, had to be large as not to be influenced by surrounding habitats. I compared our results with all the studies that Hino examined except for Nakamura (1983), because it might have used different methods from territory mapping. Instead, I added Nakamura (1986) for the comparison, a census work carried out the same deciduous forest in Kayanodaira, Nagano Prefecture. I also included Suzuki et al. (1983) and Fujimaki (1988) that generally meet the criteria, although some disturbances occurred within 100 years before the surveys. I compared breeding species number, total breeding density and total biomass presented in these six studies, 3 were from Hokkaido and 3 from Honshu (Fig. 5-1, Table 5-1), with those on Mt. Tsukuba. For the body mass of each bird species I referred to Kiyosu (1966) and Dunning (1993). For the studies of two census years, I used means. The taxonomy and nomenclature is based on the check-list of Japanese birds 6th revised edition (The Ornithological Society of Japan 2000).

This study is a joint research with Syuya Nakamura. The study design was proposed by H.T. Survey trips for the territory mapping were conducted by S.N. and H.T., alternatively, in both survey years to minimize observer bias. The banding survey were also carried out by the two. The observation in the 1-ha survey plot was conducted by S.N. Data analysis was done by H.T.

## **5-3 Results**

### **5-3-1 Territory mapping**

Thirty-seven bird species, including exotic leiothrix and the Chinese Bamboo Partridge, were recorded in the plot in the two census years. Twenty-three and 27 species were found to occupy territories in 1994 and 1995, respectively. Leiothrix was the most dominant breeding species, occupying about one third of total territories, in both years (Table 5-2). For native bird species, Bush Warbler *Cettia diphone* and Great Tit *Parus major* were dominant bird species, occupying 15% and 10%, respectively. Species of which average dominance exceeded 2% were Japanese Pygmy Woodpecker *Dendrocopos kizuki*, Brown-eared Bulbul *Hypsipetes amaurotis*, Short-tailed Warbler *Urosphena squameiceps*, Long-tailed Tit *Aegithalos caudatus*, Varied Tit *Parus varius* and Japanese White-eye. The Siberian Meadow Bunting, an edge species, had territories near Miyukigahara. Tree Sparrows *Passer montanus*, which live almost exclusively in residential areas in Japan and are seen in Miyukigahara year round, were also recorded in 1995.

### **5-3-2 Density and fates of nests**

Six complete nests were found in a 1 ha area of the plot in 1995 (Fig. 5-2). Of those, four nests contained clutches and one nest contained a destroyed eggshell. No egg was observed in the remaining one nest, possibly predated soon after laying. Other than the 6 complete nests, an incomplete nest was found in the 1 ha area. I felt that it were difficult for us to locate all the nests in the dwarf bamboo bushes even within an 1 ha area.

All males associated these territories were color banded and two of them re-nested after predation of their nests, though females were not identified in both cases. Two out of the 6

complete nests in the 1 ha area are supposed to have fledged young, and two ringed young from one nest were recaptured within the breeding season (Fig. 5-3). Of the four remaining nests, at least 3 nests had predated eggs.

Although leiothrix nest from April to September on Mt. Tsukuba (pers. obs.), the six complete nests found here were most likely to be first nesting attempts. Therefore, their density would represent minimum breeding density in early breeding season, at least 600 pairs per 100ha in this case, though sample area is small.

### **5-3-3 Comparison with Haga's list**

Our list of birds that were found in the plot lacks Common Cuckoo *Cuculus canorus* and Great-spotted Woodpecker *Dendrocopos major*, which were listed in Haga's list. The Great-spotted Woodpecker is rarely seen on Mt. Tsukuba, but in much smaller numbers than Japanese Green Woodpecker *Picus awokera*, another medium-sized woodpecker. The Common Cuckoo is basically not a bird of forest, although it is rarely heard around Miyukigahara.

I recorded three tropical migrant species, Horsfield's hawk Cuckoo *Cuculus fugax*, Siberian Thrush *Turdus sibiricus*, Pale-legged Warbler *Phylloscopus borealoides* that Haga's list lacks. While latter two species were transients, the Horsfield's hawk Cuckoo, which parasitizes on flycatchers and robins, occupied a territory in 1995.

### **5-3-4 Comparison with other Japanese deciduous forests**

The average number of breeding native bird species in the six forests compared was 26.8 (20-32.5, Fig 5-4 (1)), similar to that on Mt. Tsukuba (24). Mt. Tsukuba lacked Great-spotted Woodpecker and Nuthatch *Sitta europaea*, which bred in all six forests. From Haga's list, it is clear that the Nuthatch was absent on Mt. Tsukuba even before leiothrix invasion. The Japanese

Green Pigeon *Sphenurus sieboldii*, White's Thrush *Turdus dauma* and Brown Flycatcher *Muscicapa dauurica*, which bred in four out of the six forests, did not occupy territories on Mt. Tsukuba, although were present in the plot at least in one study years. In contrast, Japanese White-eye, a common breeder on Mt. Tsukuba, did not occupy territories in the six forests compared.

The breeding density of native birds of Mt. Tsukuba (616 pairs per 100 ha) is in the range of the six previous studies (370-620 pairs, average 505 pairs, Fig. 5-4 (2)). Including leiothrix, total breeding bird density on Mt. Tsukuba reached around 1000 pairs per 100 ha. The presence of leiothrix, thus, does not seem to depress breeding density of native birds.

Total biomass is markedly affected by presence of some large species such as Copper Pheasant *Syrmaticus soemmerringii*, which weigh about 1000 g. Again, the biomass of leiothrix (17.5 kg per 100 ha) does not seem to depress that of native birds of Mt. Tsukuba (42.3 kg), which is in the range of the six previous studies (21.5-43.5 kg, average 34.1 kg, Fig. 5-4 (3)).

#### **5-4 Discussion**

The territory mapping showed that leiothrix breed in Mt. Tsukuba at a high density, 350-400 pairs per 100 ha, which is comparable to the total breeding bird density reported in some Japanese deciduous forests (e.g., Inoue and Kondo 1983, Suzuki et al. 1983, Kobayashi and Fujimaki 1985). Such a high breeding density is uncommon for Japanese forest bird species, and the sole species comparable to this within the six studies compared is Coal Tit *Parus ater* in Kayanodaira (Nakamura 1986) which breed at 211 pairs per 100 ha, or at an even much higher density (Nakamura et al. 1987). The nest survey ascertained the high density of leiothrix and even suggested that it may be underestimated. For leiothrix that nest on dwarf bamboo bushes,

nest site is less likely to be a limiting factor of breeding density as in many hole nesters (Amano and Eguchi 2002).

It has no doubt that leiothrix have undergone a population explosion peculiar to introduced species since the first record in 1980 on Mt. Tsukuba, although details of the increase are unknown. Haga (1988) wrote that this species was seen in rather large flocks in winter. When I mist-netted in July and September 1990, leiothrix was already the most dominant species. As there were no nearby large leiothrix breeding areas from which mass immigration can occur to Mt. Tsukuba, this rapid increase was caused by successful breeding of the present population.

In spite of the high breeding density of leiothrix, the native avifauna does not seem to be altered (Fig. 5-4). Species that have disappeared in the decade are minimal, if any. The absence, or very low density, of two trunk foragers, Great-spotted Woodpecker and Nuthatch characterizes the avifauna in deciduous forest on Mt. Tsukuba, but there is little possibility that they have been excluded by leiothrix. Supposed native competitors on Mt. Tsukuba, such as Bush Warbler and Great Tit bred in higher densities than in any of leiothrix-free forests compared in this study. Both total breeding density and total biomass of native species on Mt. Tsukuba are in the range of those in the six compared forests and, therefore, do not seem to be depressed by those of leiothrix.

All-in-all, I did not find any sign of leiothrix impact on native bird species. The total avifauna of Mt. Tsukuba seems to be a simple sum of native species and a huge amount of leiothrix. Therefore, I suggest that leiothrix have invaded Mt. Tsukuba without severe competition with native bird species.

Eguchi and Masuda (1994) found similar results in Kyushu and suggest that leiothrix may have invaded into a vacant niche, a lower layer in the deciduous forests. However, it would be premature to conclude that leiothrix is harmless to native birds. Interspecific competition may

have an effect only during infrequent lean periods, as Mountainspring and Scott (1985) suggest. On the other hand, even if leiothrix have lowered breeding success of certain native bird species, breeding density of those species may change little, because enough recruit may come from surrounding “leiothrix-free” breeding areas for the species. In such cases, however, the effects on breeding density may become apparent when expanding leiothrix breeding area reached a threshold that remaining leiothrix-free breeding areas of the native species no longer produce enough recruits.

## 5-5 Figures and Tables

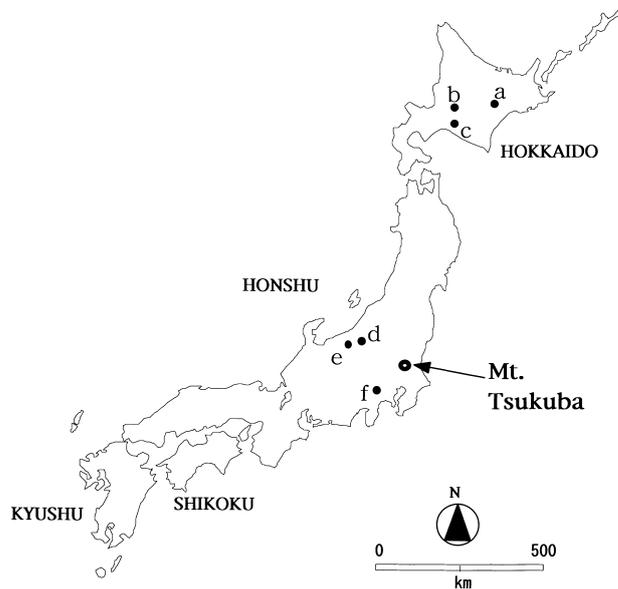


Fig. 5-1. Location of Mt. Tsukuba and study sites of referred studies. Abbreviations: a; Fujimaki (1988), b; Suzuki et al. (1983), c; Fujimaki (1986), d; Nakamura (1986), e; Mitsuishi (1970), f; Uramoto (1961).

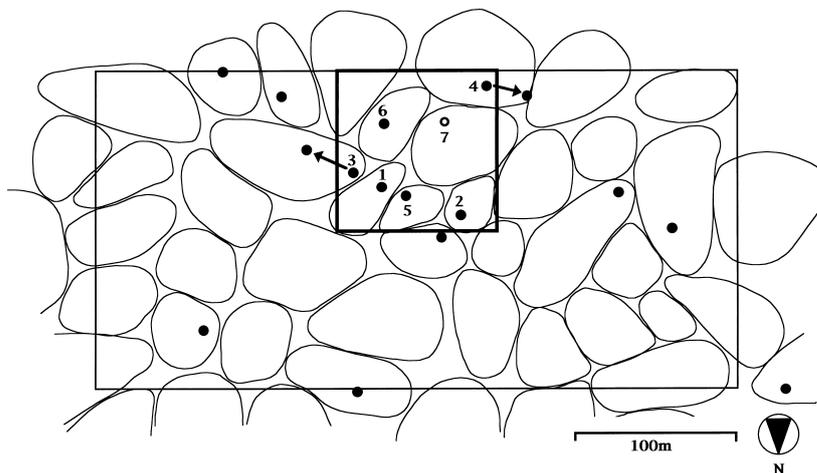


Fig. 5-2. Distribution of leiothrix territories and nests in 1995. The square shows the 1ha intensive area for nest survey. Closed circles show complete nests and an open circle shows an incomplete nest. Arrows indicate re-nesting by same males after nest predation.

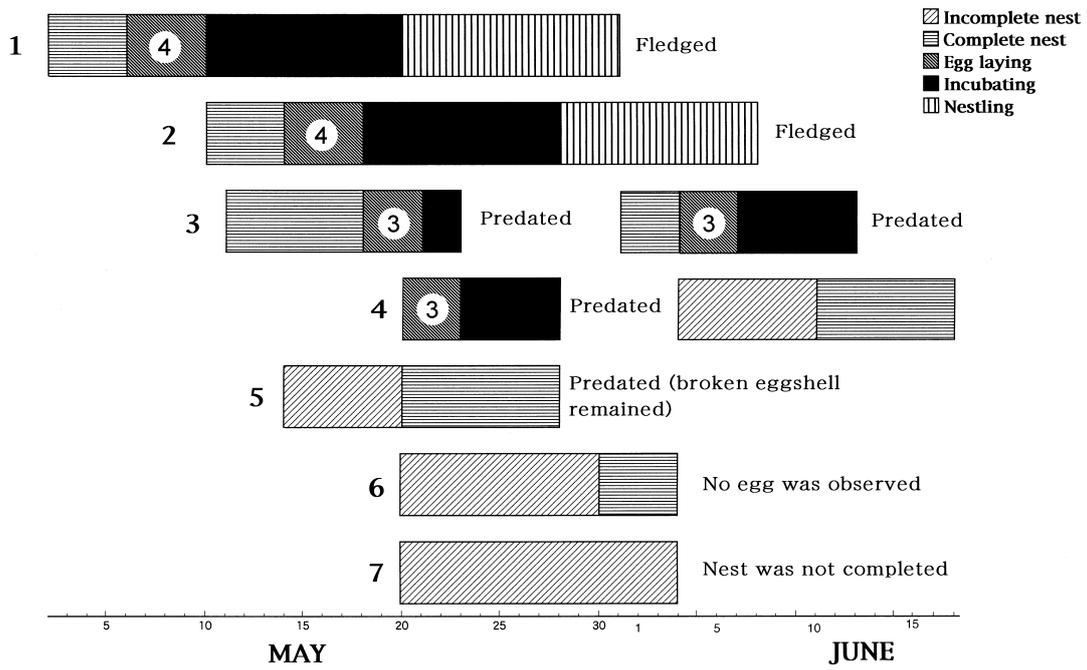


Fig. 5-3. Stages and fates of leiothrix nests in the 1 ha area in the plot. Numbers of each bar indicate nests in Fig. 5-2. Numbers in laying periods in bars show clutch size of each nests. Both two replacement nests were outside the 1ha area.

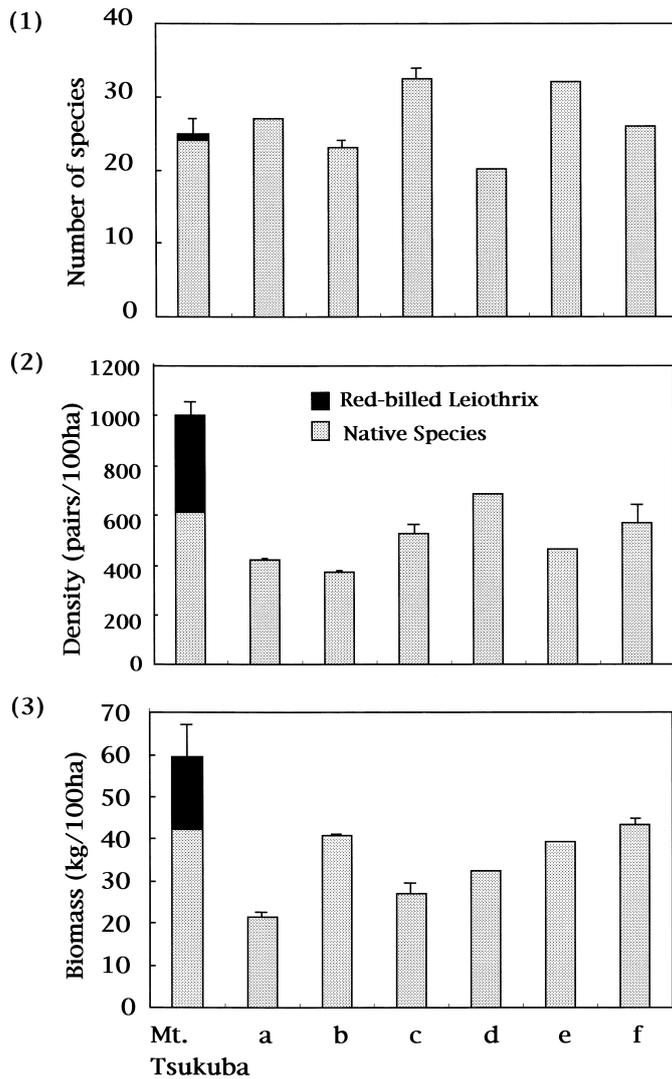


Fig. 5-4. 1) Number of species 2) total density 3) total biomass of breeding birds on Mt.

Tsukuba and in six Japanese natural deciduous forests. See Figure 5-1 for abbreviations. Bars show SD for data collected in two years.

Table 5-1. Breeding bird surveys by mapping methods in Japanese natural deciduous forests.

Source	Prefecture	Plot size	Study years	Altitude(m)	Dominant tree species
Present study	Ibaraki	8 ha	2	700-800	<i>Fagus crenata</i> , <i>Quercus crispula</i> , <i>Prunus jamasakura</i>
Fujimaki 1988	Hokkaido	24.75 ha	2	320	<i>Quercus crispula</i> , <i>Prunus sargentii</i> , <i>Lespedeza bicolor</i>
Suzuki et al. 1983	Hokkaido	15.5 ha	2	60-100	<i>Ostrya japonica</i> , <i>Acer mono</i>
Fujimaki 1986	Hokkaido	24.75 ha	2	60	<i>Quercus crispula</i> , <i>Magnolia obovata</i> , <i>Prunus sargentii</i>
Nakamura 1986	Nagano	5.7 ha	1	1460-1500	<i>Fagus crenata</i>
Mitsuishi 1970	Nagano	2986 m*	1	1200-1400	<i>Fagus crenata</i>
Uramoto 1961	Saitama	2750 m*	2	900-1200	<i>Fagus crenata</i> , <i>F. japonica</i>

\* Territories were mapped along a census belt with width determined for each bird species.

Table 5-2. Number of territories in 8 ha plot.

Family	Common name	Scientific name	1994	1995
Phasianidae	Chinese Bamboo Partridge	<i>Bambusicola thoracica*</i>	+	+
	Copper Pheasant	<i>Syrnaticus soemmerringii</i>	+	0.5
Columbidae	Rufous Turtle Dove	<i>Streptopelia orientalis</i>	1.0	0.5
	Japanese Green Pigeon	<i>Sphenurus sieboldii</i>		+
Cuculidae	Fugitive Hawk Cuckoo	<i>Cuculus fugax</i>		0.5
	Oriental Cuckoo	<i>Cuculus saturatus</i>	0.5	1.0
	Little Cuckoo	<i>Cuculus poliocephalus</i>	1.0	1.5
Picidae	Japanese Green Woodpecker	<i>Picus awokera</i>	0.5	1.0
	Japanese Pygmy Woodpecker	<i>Dendrocopos kizuki</i>	1.5	2.5
Pycnonotidae	Brown-eared Bulbul	<i>Hypsipetes amaurotis</i>	2.5	1.5
Laniidae	Bull-headed Shrike	<i>Lanius bucephalus</i>	+	
Troglodytidae	Winter Wren	<i>Troglodytes troglodytes</i>	0.5	1.0
Trudidae	Japanese Robin	<i>Erithacus akahige</i>	+	0.5
	Siberian Blue Robin	<i>Luscinia cyane</i>	1	1.5
	White's Thrush	<i>Turdus dauma</i>	+	+
	Siberian Thrush	<i>Turdus sibiricus</i>	+	
	Grey Thrush	<i>Turdus cardis</i>	1.0	0.5
Sylviidae	Short-tailed Bush Warbler	<i>Urosphena squameiceps</i>	4.5	3.5
	Bush Warbler	<i>Cettia diphone</i>	13.5	10.5
	Arctic Warbler	<i>Phylloscopus borealis</i>		+
	Eastern Pale-legged Leaf Warbler	<i>Phylloscopus borealoides</i>	+	
	Crowned Willow Warbler	<i>Phylloscopus coronatus</i>	1.0	1.0
Muscicapidae	Narcissus Flycatcher	<i>Ficedula narcissina</i>	1.0	1.5
	Blue and White Flycatcher	<i>Cyanoptila cyanomelana</i>	0.5	1.0
	Brown Flycatcher	<i>Muscicapa dauurica</i>		+
Aegithalidae	Long-tailed Tit	<i>Aegithalos caudatus</i>	2.0	3.0
Paridae	Willow Tit	<i>Parus montanus</i>	+	1.5
	Coal Tit	<i>Parus ater</i>	1.0	1.5
	Varied Tit	<i>Parus varius</i>	1.5	2.5
	Great Tit	<i>Parus major</i>	8.5	7.5
Zosteropidae	Japanese White-eye	<i>Zosterops japonicus</i>	1.5	3.0
Emberizidae	Siberian Meadow Bunting	<i>Emberiza cioides</i>	0.5	1.0
Fringillidae	Japanese Grosbeak	<i>Eophona personata</i>	1.0	0.5
Ploceidae	Tree Sparrow	<i>Passer montanus</i>		+
Corvidae	Jay	<i>Garrulus glandarius</i>	1.0	1.0
	Jungle Crow	<i>Corvus macrorhynchos</i>	+	+

Table 5-2. Number of territories in 8 ha plot. (Continued)

Family	Common name	Scientific name	1994	1995
Timaliidae	Red-billed Leiothrix	<i>Leiothrix lutea*</i>	28.5	33.5
Total number of territories			75.5	85.0
Number of species that occupied territories			23	27

Plus mark indicates presence in the plot without occupying territories

Asterisk indicates introduced species

Appendix 5-1. Avifaunal list on Mt. Tsukuba prepared by Haga. (1988)

Compared with present list			Excluded from comparison		
Family	Common name	Scientific name	*	Common name	Scientific name
Ardeidae			c	Japanese Night Heron	<i>Gorsakius goisagi</i>
Accipitridae			a	Black Kite	<i>Milvus migarans</i>
			a	Sparrowhawk	<i>Accipiter nisus</i>
			a	Grey-faced Buzzard-eagle	<i>Butastur indicus</i>
Falconidae			a	Kestrel	<i>Falco tinnunculus</i>
Phasianidae	Chinese Bamboo Partridge	<i>Bambusicola thoracica</i>	b	Pheasant	<i>Phasianus colchicus</i>
	Copper Pheasant	<i>Syrnaticus soemmerringii</i>			
Columbidae	Rufous Turtle Dove	<i>Streptopelia orientalis</i>			
	Japanese Green Pigeon	<i>Sphenurus sieboldii</i>			
Cuculidae	Common Cuckoo	<i>Cuculus canorus</i>			
	Oriental Cuckoo	<i>Cuculus saturatus</i>			
	Little Cuckoo	<i>Cuculus poliocephalus</i>			
Strigidae			c	Collared Scops Owl	<i>Otus lempiji</i>
			c	Brown Hawk Owl	<i>Ninox scutulata</i>
			c	Ural Owl	<i>Strix urarensis</i>
Caprimulgidae			c	Jungle Nightjar	<i>Caprimulgus indicus</i>
Apodidae			d	White-rumped Swift	<i>Apus pacificus</i>
Alcedinidae			e	Kingfisher	<i>Alcedo atthis</i>
Picidae	Japanese Green Woodpecker	<i>Picus awokera</i>			
	Great Spotted Woodpecker	<i>Dendrocopos major</i>			
	Japanese Pygmy Woodpecker	<i>Dendrocopos kizuki</i>			
Alaudidae			b	Skylark	<i>Alauda arvensis</i>
Hirundidae			d	House Swallow	<i>Hirundo rustica</i>
			d	Red-rumped Swallow	<i>Hirundo daurica</i>
Motacillidae			e	Grey Wagtail	<i>Motacilla cinerea</i>
			e	White Wagtail	<i>Motacilla alba</i>
			e	Japanese Wagtail	<i>Motacilla grandis</i>
			g	Olive-backed Pipit	<i>Anthus hodgsoni</i>
			f	Water Pipit	<i>Anthus spinoletta</i>
Pycnonotidae	Brown-eared Bulbul	<i>Hypsipetes amaurotis</i>			
Laniidae	Bull-headed Shrike	<i>Lanius bucephalus</i>			
Troglodytidae	Winter Wren	<i>Troglodytes troglodytes</i>			
Prunellidae			g	Alpine Accentor	<i>Prunella collaris</i>
			g	Japanese Accentor	<i>Prunella rubida</i>

Appendix.5-1. Avifaunal list on Mt. Tsukuba prepared by Haga. (1988) (Continued)

Compared with present list			Excluded from comparison		
Family	Common name	Scientific name	*	Common name	Scientific name
Trudidae	Japanese Robin	<i>Erithacus akahige</i>	g	Red-flanked Bushrobin	<i>Tarsiger cyanurus</i>
	Siberian Blue Robin	<i>Luscinia cyane</i>	f	Daurian Redstart	<i>Phoenicurus aureoreus</i>
	White's Thrush	<i>Turdus dauma</i>	g	Brown Thrush	<i>Turdus chrysolaus</i>
	Grey Thrush	<i>Turdus cardis</i>	f	Pale Thrush	<i>Turdus pallidus</i>
			f	Dusky Thrush	<i>Turdus naumanni</i>
Sylviidae	Short-tailed Bush Warbler	<i>Urosphena squameiceps</i>	g	Goldcrest	<i>Regulus regulus</i>
	Bush Warbler	<i>Cettia diphone</i>			
	Arctic Warbler	<i>Phylloscopus borealis</i>			
	Crowned Willow Warbler	<i>Phylloscopus coronatus</i>			
Muscicapidae	Narcissus Flycatcher	<i>Ficedula narcissina</i>			
	Blue and White Flycatcher	<i>Cyanoptila cyanomelana</i>			
	Brown Flycatcher	<i>Muscicapa dauurica</i>			
Aegithalidae	Long-tailed Tit	<i>Aegithalos caudatus</i>			
Paridae	Willow Tit	<i>Parus montanus</i>			
	Coal Tit	<i>Parus ater</i>			
	Varied Tit	<i>Parus varius</i>			
	Great Tit	<i>Parus major</i>			
Zosteropidae	Japanese White-eye	<i>Zosterops japonicus</i>			
Emberizidae	Siberian Meadow Bunting	<i>Emberiza cioides</i>	f	Rustic Bunting	<i>Emberiza rustica</i>
			g	Black-faced Bunting	<i>Emberiza spodocephala</i>
			g	Grey Bunting	<i>Emberiza variabilis</i>
Fringillidae	Japanese Grosbeak	<i>Eophona personata</i>	f	Brambling	<i>Fringilla montifringilla</i>
			b	Oriental Greenfinch	<i>Carduelis sinica</i>
			f	Siskin	<i>Carduelis spinus</i>
			f	Rosy Finch	<i>Leucosticte arctoa</i>
			f	Long-tailed Rosefinch	<i>Uragus sibiricus</i>
			g	Bullfinch	<i>Pyrrhula pyrrhula</i>
			f	Hawfinch	<i>Coccothraustes coccothraustes</i>
Ploceidae	Tree Sparrow	<i>Passer montanus</i>			
Sturnidae			b	Grey Starling	<i>Sturnus cineraceus</i>
Corvidae	Jay	<i>Garrulus glandarius</i>	b	Azure-winged Magpie	<i>Cyanopica cyana</i>
	Jungle Crow	<i>Corvus macrorhynchos</i>	b	Carrion Crow	<i>Corvus corone</i>
Total number of species		35			41

\*reasons for exclusions: a:raptors, b:farmland species, c:nocturnal species, d:aerial species,

e: aquatic species, f:not breed in central Japan, g: breed in higher altitudinal areas

## **Chapter 6 General Discussion**

## **Chapter 6 General Discussion**

### **6-1 Pattern of Bird Species Diversity in Cool-temperate Deciduous Forests**

In chapters 2 and 3, I tried to characterize general patterns of bird species diversity in Japanese cool-temperate deciduous forests. I documented seasonality of bird species diversity (Chapter 2) and breeding bird community (Chapter 3) of the Ogawa Forest Reserve, one of the most preserved forests in the region. Then I generalized the results by comparing them with seasonal patterns in other studies including those conducted in other natural forest types (Chapter 2) and, with bird communities in other Japanese deciduous forests (Chapter 3).

Chapter 2 showed that the seasonal pattern of bird community in cool-temperate deciduous forests has a peak in autumn migrating season and pointed out for the first time the importance of this forest type as stopover sites for migrants. In contrast with this forest type, subarctic mixed forests, which are typical natural forests in Hokkaido, are not widely used by migrants during the non-breeding season, most likely because of the harsh climatic conditions. On the other hand, warm-temperate evergreen forests are widely used by birds during both autumn migration and winter seasons, and bird diversity were generally high in winter than in breeding season.

Unfortunately, non-breeding seasons have been ignored by many studies on conservation of bird species diversity. However, the differences in seasonality suggested that each potential natural forest type plays unique role in providing habitats for migrant bird species. This, in turn, would imply that even among similar secondary or plantation forests, the role as habitats for migrant birds may be different, depending on the vegetation zone the forest belongs to. For example, Japanese cedar plantations in warm-temperate forest zone should be managed to be good wintering habitats, while similar plantations in cool-temperate zone to be good

habitats during breeding and autumn migrating seasons. The habitat quality during migrating or wintering season would be evaluated, for example, by the dominance of plants that fruit at appropriate timing (Masaki et al. 1994, Noma and Yumoto 1997, Naoe et al. 2011). The interactions between plants and birds are important in terms of ecological service, which may enhance biodiversity (Whelan et al. 2015, Şekerciöğlü et al. 2016).

Chapter 3 documented spatial variability of the bird species diversity among Japanese cool-temperate deciduous forests, and showed that the elevation had the most significant effects on bird species diversity, while the other geographical variables (latitude and longitude) did not have significant effects. Therefore, bird species diversity of the OFR represents low-montane broad-leaved deciduous forests in Honshu, and would be a valuable sample from the area that has been severely disturbed by human activities.

In montane regions of Japan, forest reserves tend to be established in high altitudinal areas where the slopes are steep and commercial forestry is hardly practicable. However, my results suggested the need for setting protected forests even in low-montane areas as bird communities of these forests were different from those in high-montane areas.

## **6-2 Effects of Forest Fragmentation on Bird Species Diversity**

In chapter 4, I focused on a fine mozaic landscape of conifer plantations and broad-leaved secondary forests with various ages and examined effects of stand type and age on bird diversity. Both species richness and abundance increased with age in both conifer and broad-leaved forests, but decreased in old-growth stage (over 100 year). On the other hand, forest type did not had significant effects on bird diversity in terms of species richness and abundance, a result conflicting with a dominant view that conifer plantations have poorer bird communities than broad-leaved forests (e.g., Lindenmayer and Hobbs 2004, Yamaura et al. 2006, Yamaura 2007).

However, the CCA ordination showed that the conifer plantations and broad-leaved forests differed in the species composition they had, and that the mature and old-growth deciduous stands were important for preserving bird species diversity within the landscape because they harbored rare species.

The results also made me focus on the function as potential bird habitats of a plantation species, the Japanese cedar, a native species that distributed widely over the Japanese Archipelago (Tsukada 1982, Uchiyama 2003, Tsumura et al. 2012, Kimura et al. 2014). Recently, more than half of Japanese plantations are exceeding the age appropriate to be harvested (Forestry Agency of Japan 2015), and we have to consider how to manage these “mature and old-growth plantations” so that they contribute to preserving biodiversity. Examining bird diversity in remnant natural Japanese cedar forests (e.g., Eguchi et al. 1989, Eguchi et al. 1992), as well as research on arthropods on the Japanese cedar for bird food (Hijii 1989, Hijii et al. 2001, Mizutani and Hijii 2002) would help understand the potential of this tree species as surrogate broad-leaved trees.

### **6-3 Invasion by Alien Birds into Natural Deciduous Forests**

In chapter 5, I studied a population of an alien bird species, the Red-billed Leiothrix. My results cautioned that even in a preserved deciduous forest, bird species diversity could be drastically changed by the invasion of alien species. Although negative impacts on native bird species were not detected in this study, given its high breeding density, Leiothrix could have impacts on native ecosystems through, for example, seed dispersal (Tojo and Nakamura 1999). Furthermore, this species might have affected on native Japanese Bush Warbler through predator-mediated interactions or “apparent competition” (Eguchi and Amano 2008).

In the study area of northern Ibaraki, the Red-billed Leiothrixes and the Chinese Hwamei were recorded in the present study (Chapter 4). To my knowledge, the Red-billed Leiothrix was firstly recorded in this area, suggesting distributional expansion of this species. The data showed that these alien species became common components of forest bird diversity in Japan. However, these exotic species do not contribute to the evaluation of biodiversity, as indicators for biodiversity include only native species (e.g., Forestry Agency of Japan 2009).

Recently, eradication projects of alien species, such as the Small Indian Mongoose *Herpestes auropunctatus* (Watari et al. 2013) and the Canada Goose *Branta canadensis* (Ministry of the Environment of Japan 2015), have been successful in Japan. Unfortunately, however, eradication of small alien birds, such as the Red-billed Leiothrix, is very difficult once it had established. Import ban of invasive alien species and early eradication before establishment are, therefore, essential.

#### **6-4 Conclusion**

This thesis investigated the bird species diversity in Japanese cool-temperate broad-leaved deciduous forests, and its temporal and spatial variability. The seasonality of bird diversity in the cool-temperate deciduous forests suggested that this forest type provided important stopover sites for migratory birds. Given the importance of wintering and stopover sites for the conservation of migrants, evaluation of bird species diversity in non-breeding season should not be omitted. As bird communities in the Japanese deciduous forests significantly varied with elevation, forest reserves should not concentrate in high altitudinal areas to preserve low-montane species. The study on a fragmented forest landscape showed that in terms of species richness and abundance, conifer plantations harbored diverse bird communities comparable to broad-leaved stands. For preserving bird species diversity in the landscape,

however, mature and old-growth deciduous forests seemed important, as they harbored rare species. The study on the Red-billed Leiothrix documented that an alien species had become most dominant bird species in natural deciduous forests. As no control methods are available for these small alien birds, prevention of establishment seemed essential.

## **Abstract of thesis**

The preservation of biological diversity is one of the most important priorities of sustainable forest management and birds are useful indicators of forest biodiversity. The cool-temperate broad-leaved deciduous forest is one of typical forest types in Japan. However, there are serious threats to bird species diversity living there: 1) loss of primeval forests has caused disappearance of rare species and obscured the original biodiversity of this forest type, 2) forest fragmentation has altered the forest areas to mosaic of small forest patches with various ages and types, and 3) alien species invasion may affect native ecosystems. In this thesis, I conducted four field surveys to study these three issues and discussed the results and provided recommendations for the conservation and management of bird species diversity in deciduous forests.

In chapter 2, I surveyed the seasonality of bird community in the Ogawa Forest Reserve, an old-growth deciduous forest in central Japan. Both species richness and total bird abundance were lowest in mid-winter and peaked in spring breeding season, remaining high during autumn migrating season. An ordination using non-metric multidimensional scaling showed that the bird community varied more during the non-breeding season than during the breeding season. Comparisons of the seasonal patterns of bird communities with other types of natural forests showed that cool-temperate deciduous forests had highly diverse avifauna during autumn, suggesting that such forests are important stopover sites for migrants.

In chapter 3, I documented the breeding bird community of the Ogawa Forest Reserve. The results suggested that the OFR harbored a diverse breeding bird community including many red-listed species. Cluster and ordination analyses indicated that the avifauna of the OFR was characterized more by the elevation than by the geographic location and thus represented the

bird species diversity of low-montane broad-leaved deciduous forests of Honshu. As low-montane areas of Japan have been degraded in recent decades, data on the bird species biodiversity obtained there should be useful for sustainable forest management.

In chapter 4, the effects of stand age and type on bird species diversity were studied in northern Ibaraki, central Japan. The GLMM models for the species richness and abundance and GLM models for cumulative species richness selected based on AIC were contained stand age and its quadric terms as explanatory variables. All the three response variables showed unimodal curves with respect to stand age, increasing with stand age toward approx. 100 years and then decreasing in older stands. A Canonical Correspondence Analysis (CCA) divided the 21 study plots into three groups, 1) early successional stage, 2) conifer plantations and 3) broad-leaved stands. Six out of eight red-listed species preferred the broad-leaved stands. The results suggested that although conifer plantations supported diverse bird communities comparable to broad-leaved stands in terms of species richness and abundance, mature and old-growth broad-leaved forests were important to increase bird diversity at the landscape level, because they harbored rare species.

In chapter 5, the breeding densities of exotic Red-billed Leiothrix and native bird species were investigated on Mt. Tsukuba (877m), central Japan. The Red-billed Leiothrix bred at very high density (350-400 pairs per 100 ha) and was the most dominant species. Despite the high breeding density of leiothrix, the species diversity, total breeding density and total biomass of native birds were similar to those in other Japanese deciduous forests. Therefore, I suggested that leiothrix had invaded Mt. Tsukuba without severe competition with native bird species.

In chapter 6, I discussed the results and proposed management recommendations. (1) As the cool-temperate deciduous forests provide important stopover sites for migratory birds, bird diversity in non-breeding season should be monitored and evaluated. (2) Forest reserves

should not be concentrated in high-altitudinal areas to conserve low-mountain species. (3) For preserving bird species diversity of an area at the landscape level, the mature and old-growth deciduous forests are critical. (4) Prevention of establishment of small alien birds is essential because they may become the most dominant species even in natural deciduous forests and, so far, no control methods are available.

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## References

- Ali, S. 1977. Field Guide to the Birds of the Eastern Himalayas. Oxford University Press, Delhi.
- Amano, H. E., and K. Eguchi. 2002. Nest-site selection of the Red-billed Leiothrix and Japanese Bush Warbler in Japan. *Ornithological Science* **1**:101-110.
- Amano, T., and Y. Yamaura. 2007. Ecological and life-history traits related to range contractions among breeding birds in Japan. *Biological Conservation* **137**:271-282.
- Askins, R. A., H. Higuchi, and H. Murai. 2000. Effect of forest fragmentation on migratory songbirds in Japan. *Global Environmental Research* **4**:219-229.
- Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. *Current Ornithology* **7**:1-57.
- Bayly, N. J., and C. Gómez. 2011. Comparison of autumn and spring migration strategies of Neotropical migratory landbirds in northeast Belize. *Journal of Field Ornithology* **82**:117-131.
- Berger, A. J. 1981. Hawaiian Birdlife. 2nd edition. University Press of Hawaii, Honolulu.
- Bestelmeyer, B. T., J. R. Miller, and J. A. Wiens. 2003. Applying species diversity theory to land management. *Ecological Applications* **13**:1750-1761.
- Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. Bird Census Techniques. Academic Press, London.
- Bibby, C. J., N. D. Burgess, D. A. Hill, and S. H. Mustoe. 2000. Bird Census Techniques, 2nd Edition. Academic Press, London.
- Birdlife International. 2000. Threatened Birds of the World. Lynx Edicions and Birdlife International, Barcelona and Cambridge.
- Blackburn, T. M., J. L. Lockwood, and P. Cassey. 2009. Avian Invasions : the Ecology and Evolution of Exotic Birds. Oxford University Press, Oxford.

- Böhning-Gaese, K., and H.-G. Bauer. 1996. Changes in species abundance, distribution, and diversity in a central European bird community. *Conservation Biology* **10**:175-187.
- Case, T. J. 1996. Global patterns in the establishment and distribution of exotic birds. *Biological Conservation* **78**:69-96.
- del Hoyo, J., and N. J. Collar. 2016. *HBW and BirdLife International Illustrated Checklist of the Birds of the World. Volume 2: Passerines*. Lynx Edicions, Barcelona.
- Diamond, J. M., and C. R. Veitch. 1981. Extinctions and introductions in the New Zealand avifauna : Cause and effect? *Science* **211**:499-501.
- Dunning, J. B., Jr. 1993. *CRC Handbook of Avian Body Masses*. CRC Press, Boca Raton.
- Ecological Society of Japan. 2002. *Handbook of Alien Species in Japan*. Chijinshokan, Tokyo (in Japanese).
- Eguchi, K., and H. E. Amano. 2000. Problems of introduction and naturalizations in birds. *Japanese Journal of Conservation Ecology* **5**:131-148 (in Japanese with English summary).
- Eguchi, K., and H. E. Amano. 2004. Invasive birds in Japan. *Global Environmental Research* **8**:29-39.
- Eguchi, K., and H. E. Amano. 2008. Indirect influences of the invasive Red-billed Leiothrix on the breeding of the Japanese Bush Warbler. *Japanese Journal of Ornithology* **57**:3-10 (in Japanese with English summary).
- Eguchi, K., and T. Masuda. 1994. A report on the habitats of Peking Robin *Leiothrix lutea* in Kyushu. *Japanese Journal of Ornithology* **43**:91-100 (in Japanese with English summary).
- Eguchi, K., M. Takeishi, H. Nagata, and Y. Henmi. 1992. Altitudinal distribution of forest birds in the Yaku-shima island, Kagoshima Prefecture, Japan. II . Non-breeding season.

- Japanese Journal of Ecology **42**:107-113 (in Japanese with English summary).
- Eguchi, K., M. Takeishi, H. Nagata, Y. Henmi, and N. Kawaji. 1989. Altitudinal distribution of forest birds in the Yaku-shima island, Kagoshima Prefecture, Japan. I. Breeding season. Japanese Journal of Ecology **39**:53-65 (in Japanese with English summary).
- Emlen, J. T. 1971. Population densities of birds derived from transect counts. The Auk **88**:323-342.
- Forestry Agency of Japan. 2009. State of Japan's Forests and Forest Management -2nd Country Report of Japan to the Montreal Process. Forestry Agency of Japan, Tokyo.
- Forestry Agency of Japan. 2015. Annual Report on Forest and Forestry in Japan Fiscal Year 2015 (Summary). Forestry Agency of Japan, Tokyo.
- Fujimaki, Y. 1970. An avifaunal study in different types of forests in the central part of Hokkaido, Japan. Bulletin of the Hokkaido Forest Experiment Station **8**:41-51 (in Japanese with English summary).
- Fujimaki, Y. 1973. The birds of Bibai, central Hokkaido. 1. Time of occurrences and habitats of birds. Tori **22**:38-46 (in Japanese with English summary).
- Fujimaki, Y. 1986. Breeding bird community in a deciduous broad-leaved forest in southern Hokkaido, Japan. Japanese Journal of Ornithology **35**:15-23 (in Japanese with English summary).
- Fujimaki, Y. 1988. Breeding bird community of a *Quercus mongolica* forest in eastern Hokkaido, Japan. Japanese Journal of Ornithology **37**:69-75 (in Japanese with English summary).
- Fukamachi, K., S. Iida, and T. Nakashizuka. 1996. Landscape patterns and plant species diversity of forest reserves in the Kanto region, Japan. Vegetatio **124**:107-114.
- Fuller, R. J., D. G. Noble, K. W. Smith, and D. Vanhinsbergh. 2005. Recent declines in

- populations of woodland birds in Britain: a review of possible causes. *British Birds* **98**:116-143.
- Furness, R. W., and J. J. D. Greenwood. 1993. *Birds as Monitors of Environmental Change*. Chapman & Hall, London.
- Greenwood, J. J. D., S. R. Baillie, H. Q. P. Crick, J. H. Marchant, and W. J. Peach. 1993. Integrated population monitoring: detecting the effects of diverse changes. Pages 267-342 in R. W. Furness and J. J. D. Greenwood, editors. *Birds as Monitors of Environmental Change*. Chapman & Hall, London.
- Haga, K. 1988. Faunistic notes on Mt. Tsukuba. *Nihon no seibutu* **2**:35-41 (in Japanese).
- Hamada, T., S. Sato, and Y. Okai. 2006. Records and evidence of breeding of Ashy Laughing Thrush *Garrulax cineraceus* on Shikoku Island. *Japanese Journal of Ornithology* **55**:105-109 (in Japanese with English summary).
- Hewson, C. M., A. Amar, J. A. Lindsell, R. M. Thewlis, S. Butler, K. Smith, and R. J. Fuller. 2007. Recent changes in bird populations in British broadleaved woodland. *Ibis* **149**:14-28.
- Higuchi, H., and E. Morishita. 1999. Population declines of tropical migratory birds in Japan. *Actinia* **12**:51-59.
- Hijii, N. 1989. Arthropod communities in a Japanese cedar (*Cryptomeria japonica* D. Don) plantation: Abundance, biomass and some properties. *Ecological Research* **4**:243-260.
- Hijii, N., Y. Umeda, and M. Mizutani. 2001. Estimating density and biomass of canopy arthropods in coniferous plantations: an approach based on a tree-dimensional parameter. *Forest Ecology and Management* **144**:147-157.
- Hino, T. 1990. Palaearctic deciduous forests and their bird communities : Comparisons between East Asia and West-Central Europe. Pages 87-94 in A. Keast, editor. *Biogeography and*

- Ecology of Forest Bird Communities. SPB Academic Publishing bv, Hague.
- Hino, T. 1993. Chourui sou to sono bunpu [Avifauna and its distribution]. Pages 184-197 in S. Higashi, H. Abe, and T. Tsujii, editors. Seitaiaku kara Mita Hokkaido. Hokkaido University Publishing, Sapporo (in Japanese).
- Hino, T. 2000. Breeding bird community and vegetation structure in a forest with a high density of Sika deer. Japanese Journal of Ornithology **48**:197-204.
- Hutto, R. L., S. M. Pletschent, and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding season use. The Auk **103**:593-602.
- Ibaraki Prefectural Forest Experiment Station. 1980. Map of Actual Vegetation of Ibaraki Prefecture. Ibaraki Prefecture, Mito (in Japanese).
- Ibaraki Prefecture. 2000. Red-data Book of Ibaraki Prefecture (Animals). Ibaraki Prefecture, Mito (in Japanese).
- Imanishi, S. 2002. The drastic decline of breeding population on Brown Shrike *Lanius cristatus superciliosus* at Nobeyama Plateau in central Japan. Journal of Yamashina Institute for Ornithology **34**:228-231 (in Japanese with English summary).
- Inoue, M. 1990. The influence of clear cutting on breeding bird community of broad leaved forest in southwest Japan. Bulletin of Tottori Prefecture Forest Experiment Station **33**:39-57 (in Japanese with English summary).
- Inoue, M., and H. Hashizume. 1990. A comparison of winter bird communities between coniferous and broad-leaved forests in the Hiruzen Experimental Forest of Tottori University. Research Bulletin of the Tottori University Forests **20**:47-70 (in Japanese with English summary).
- Inoue, M., and Y. Kondo. 1983. A comparison of breeding bird communities in coniferous and broad-leaved woods. Hard-Wood Research **2**:55-72 (in Japanese with English summary).

- Ishii, S. 1992. Tsukubasan no sousichou [Red-billed Leiothrix on Mt. Tsukuba]. Page 101  
Tsukubasan. STEP, Tsukuba (in Japanese).
- Kanai, Y., R. Kurosawa, M. Ueta, M. Narusue, and M. Kamata. 1996. Forest type and birds. The  
first result of the "Monitoring Program on Birds and their Habitats". *Strix* **14**:33-39 (in  
Japanese with English summary).
- Kaneko, Y. 1981. Seasonal changes in a lowland bird community in Niigata Pref., Japan. *Tori*  
**30**:37-43 (in Japanese with English summary).
- Karasawa, K. 1971. Seasonal changes of bird community in the Boso Hills. *Tori* **20**:247-267 (in  
Japanese with English summary).
- Kawakami, K., and Y. Yamaguchi. 2004. The spread of introduced Melodious Laughing Thrush  
*Garrulax canorus* in Japan. *Ornithological Science* **3**:13-21.
- Kimura, M. K., K. Uchiyama, K. Nakao, Y. Moriguchi, L. San Jose-Maldia, and Y. Tsumura.  
2014. Evidence for cryptic northern refugia in the last glacial period in *Cryptomeria*  
*japonica*. *Annals of Botany* **114**:1687-1700.
- Kittredge, J., D. B. 1996. Changes in global forest distribution. Pages 37-60 in R. M. DeGraaf  
and R. I. Miller, editors. *Conservation of Faunal Diversity in Forested Landscape*.  
Chapman & Hall, London.
- Kiyosu, Y. 1966. *Encyclopedia of Wild Birds*. Tokyo-do Shuppan, Tokyo (in Japanese).
- Kiyosu, Y. 1978. *The Birds of Japan II, Revised and Enlarged Edition*. 2nd edition. Kodansha,  
Tokyo (in Japanese ).
- Kobayashi, S., and Y. Fujimaki. 1985. Breeding bird community in a deciduous broad-leaved  
wood and a larch plantation. *Tori* **34**:57-63 (in Japanese with English summary).
- Koskimies, P., and R. A. Väisänen. 1991. *Monitoring Bird Populations: A Manual of Methods*  
Applied in Finland. Zoological Museum. Finnish Museum of Natural History.

University of Helsinki, Helsinki.

- Kremsater, L., and F. L. Bunnell. 1999. Edge effects: Theory, evidence and implications to management of western North American forests. Pages 117-153 *in* J. A. Rochelle, L. A. Lehmann, and J. Wisniewski, editors. *Forest Fragmentation. Wildlife and Management Implications*. Brill, Leiden.
- Kurosawa, R., and R. A. Askins. 1999. Differences in bird communities on the forest edge and in the forest interior: Are there forest-interior specialists in Japan? *Journal of Yamashina Institute for Ornithology* **31**:63-79.
- Kurosawa, R., and R. A. Askins. 2003. Effects of habitat fragmentation on birds in deciduous forests in Japan. *Conservation Biology* **17**:695-707.
- Kwok, H. K., and R. T. Corlett. 1999. Seasonality of a forest bird community in Hong Kong, South China. *Ibis* **141**:70-79.
- Lampila, P., M. Mönkkönen, and A. Desrochers. 2005. Demographic responses by birds to forest fragmentation. *Conservation Biology* **19**:1537-1546.
- Lepš, J., and P. Šmilauer. 2003. *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge University Press, Cambridge.
- Lever, C. 1994. *Naturalized Animals*. T & AD Poyser, London.
- Lever, C. 2005. *Naturalised Birds of the World*. T & A.D. Poyser, London.
- Lidicker, W. Z., Jr., and W. D. Koenig. 1996. Responses of terrestrial vertebrates to habitat edges and corridors. Pages 85-109 *in* D. R. McCullough, editor. *Metapopulations and Wildlife Conservation*. Island Press, Washington D.C.
- Lindenmayer, D. B., and R. J. Hobbs. 2004. Fauna conservation in Australian plantation forests – a review. *Biological Conservation* **119**:151-168.
- Long, J. L. 1981. *Introduced Birds of the World*. David & Charles, Newton Abott.

- MacKinnon, J., and K. Phillipps. 2000. A Field Guide to the Birds of China. Oxford University Press, Oxford.
- Masaki, T. 2002. Structure and dynamics. Pages 53-65 in T. Nakashizuka and Y. Matsumoto, editors. Diversity and Interaction in a Temperate Forest Community; Ogawa Forest Reserve of Japan. Springer-Verlag, Tokyo.
- Masaki, T., Y. Kominami, and T. Nakashizuka. 1994. Spatial and seasonal patterns of seed dissemination of *Cornus controversa* in a temperate forest. *Ecology* **75**:1903-1910.
- Masaki, T., W. Suzuki, K. Niiyama, S. Iida, H. Tanaka, and T. Nakashizuka. 1992. Community structure of a species-rich temperate forest, Ogawa Forest Reserve, central Japan. *Vegetatio* **98**:97-111.
- Matsuoka, S., and Y. Takada. 1999. The role of snags in the life of woodpeckers and snag management in a forest: a review. *Japanese Journal of Ornithology* **47**:33-48 (in Japanese with English summary).
- McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Gleneden Beach, OR, USA.
- McLellan, C. H., A. P. Dobson, D. S. Wilcove, and J. F. Lynch. 1986. Effects of forest fragmentation on New and Old-World bird communities: Empirical observations and theoretical implications. Pages 305-313 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press, Madison.
- Mikusiński, G., M. Gromadzki, and P. Chylarecki. 2001. Woodpeckers as indicators of forest bird diversity. *Conservation Biology* **15**:208-217.
- Ministry of the Environment Japan. 2002. Threatened Wildlife of Japan -Red Data Book 2nd ed.- Volume 2, Aves. Japan Wildlife Research Center, Tokyo (in Japanese with English

summary).

Ministry of the Environment of Japan. 2004. The sixth national survey on the natural environment: report of the distributional survey of breeding area of Japanese birds. Ministry of the Environment, Tokyo (in Japanese ).

Ministry of the Environment of Japan. 2015. On the eradication of the Canada Goose, an invasive species as defined by law, from Japan. (in Japanese).

Mitsuishi, H. 1970. Ecological study of the bird community in Okusobana Natural Garden, Nagano Prefecture. Bulletin Institute of Nature Education, Shiga Heights, Shinshu University **9**:1229-1238 (in Japanese with English summary).

Mizutani, M., and N. Hijii. 2002. The effects of arthropod abundance and size on the nestling diet of two *Parus* species. Ornithological Science **1**:71-80.

Mönkkönen, M., and P. Helle. 1989. Migratory habits of birds breeding in different stages of forest succession: a comparison between Palaearctic and the Nearctic. Annals Zoology Fennici **26**:323-330.

Mönkkönen, M., P. Helle, and D. Welsh. 1992. Perspectives on Palaearctic and Nearctic bird migration; comparisons and overview of life-history and ecology of migrant passerines. Ibis **134**:7-13.

Mönkkönen, M., and D. Welsh. 1994. A biogeographical hypothesis of the effects of human caused landscape changes on the forest bird communities of Europe and North America. Annals Zoology Fennici **31**:61-70.

Mountainspring, S., and M. Scott. 1985. Interspecific competition among Hawaiian forest birds. Ecological Monographs **55**:219-239.

Nakamura, H. 1986. Ecological studies of the beech forest bird community on Kayanodaira Heights. Bulletin of the Institute of Nature Education in Shiga Heights, Shinshu

- University **23**:9-20 (in Japanese with English summary).
- Nakamura, H., K. Murayama, A. Kubokawa, R. Suzuki, T. Takizawa, and K. J. Shigemori. 1987. Bird community in the Kayanodaira Scientific Reserved Beech Forest in breeding season. Bulletin of the Institute of Nature Education in Shiga Heights, Shinshu University **24**:33-41 (in Japanese with English summary).
- Nakamura, K., Y. Murofushi, K. Adachi, and T. Hatsusegawa. 1993. A note on the naturalization of the Masked Laughing Thrush, *Garrulax perspicillatus* (Gmelin) , in Kanagawa Prefecture. Natural History Report of Kanagawa **14**:27-31 (in Japanese with English summary).
- Nakamura, T. 1977. Birds' community of the mature beech forest in Kayanodaira. Bulletin of the Institute of Nature Education in Shiga Heights, Shinshu University **16**:5-29.
- Nakamura, T. 1983. On the breeding bird community structure in the mature beech forest, Kayanodaira. Pages 301-307 in N. Taiga, editor. Gendai Seitaijaku no Danmen [A Profile of Modern Ecology]. Kyouritu Shuppan, Tokyo (in Japanese).
- Nakashizuka, T. 2002. Disturbance regimes. Pages 68-80 in T. Nakashizuka and Y. Matsumoto, editors. Diversity and Interaction in a Temperate Forest Community: Ogawa Forest Reserve of Japan. Springer-Verlag, Tokyo.
- Nakashizuka, T., and Y. Matsumoto. 2002. Diversity and Interaction in a Temperate Forest Community : Ogawa Forest Reserve of Japan. Springer, Tokyo.
- Naoe, S., S. Sakai, A. Sawa, and T. Masaki. 2011. Seasonal difference in the effects of fragmentation on seed dispersal by birds in Japanese temperate forests. Ecological Research **26**:301-309.
- Newton, I. 1967. The adaptive radiation and feeding ecology of some British finches. Ibis **109**:33-98.

- Newton, I. 2003. Geographical patterns in bird migration. Pages 211-224 *in* P. Berthold, E. Gwinner, and R. Sonnenschein, editors. Avian Migration. Springer-Verlag, Berlin.
- Newton, I. 2004. Population limitation in migrants. *Ibis* **146**:197-226.
- Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology* **147**:146-166.
- Newton, I. 2008. *The Migration Ecology of Birds*. 1st edition. Academic Press, Amsterdam.
- Newton, I., and L. Dale. 1996a. Relationship between migration and latitude among west European birds. *Journal of Animal Ecology* **65**:137-146.
- Newton, I., and L. C. Dale. 1996b. Bird migration at different latitudes in eastern North America. *The Auk* **113**:626-635.
- Nilsson, S. G. 1974. Methods of estimating bird population densities during the winter. *Ornis Scandinavica* **5**:37-46.
- Noma, N., and T. Yumoto. 1997. Fruiting phenology of animal-dispersed plants in response to winter migration of frugivores in a warm temperate forest on Yakushima Island, Japan. *Ecological Research* **12**:119-129.
- Numata, M. 1974. *The Flora and Vegetation of Japan*. Kodansha Limited, Tokyo.
- Oka, T., and M. Nakamura. 1998. Avifauna on the campus of Joetsu University of Education during in the non-breeding season -Effect of snow on bird community in an area of heavy snowfall-. *Strix* **16**:55-66 (in Japanese with English summary).
- Oksanen, J. 2013. *Multivariate Analysis of Ecological Communities in R: Vegan Tutorial*.
- Opdam, P. 1991. Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. *Landscape Ecology* **5**:93-106.
- Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* **8**:17-26.

- R Development Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in Neotropical birds. *American Naturalist* **149**:875-902.
- Ralph, C. J., S. G. Fancy, and T. D. Male. 1998. Demography of an introduced Red-billed Leiothrix population in Hawaii. *Condor* **100**:468-473.
- Rappole, J. H. 1996. The importance of forest for the world's migratory bird species. Pages 389-406 *in* R. M. DeGraaf and R. I. Miller, editors. *Conservation of Faunal Diversity in Forested Landscape*. Chapman & Hall, London.
- Reynolds, R. T., J. M. Scott, and R. A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. *Condor* **82**:309-313.
- Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**:1987-1990.
- Şekercioğlu, Ç. H., D. G. Wenny, and C. J. Whelan. 2016. *Why Birds Matter: Avian Ecological Function and Ecosystem Services*. The University of Chicago Press, Chicago.
- Shibata, M., and H. Tanaka. 2002. Reproductive traits of trees in OFR. Pages 95-108 *in* T. Nakashizuka and Y. Matsumoto, editors. *Diversity and Interaction in a Temperate Forest Community: Ogawa Forest Reserve of Japan*. Springer-Verlag, Tokyo.
- Shiu, H. J., and P. F. Lee. 2003. Seasonal variation in bird species richness along elevational gradients in Taiwan. *Acta Zoologica Taiwanica* **14**:1-21.
- Suzuki, T., S. Saito, and M. Saito. 1983. Bird populations during the breeding season in a deciduous broad-leaved forest at Iwamizawa, central Hokkaido. *Bulletin of the Hokkaido Forest Experiment Station* **21**:95-103 (in Japanese with English summary).

- Suzuki, W. 2002. Forest vegetation in and around Ogawa Forest Reserve in relation to human impact. Pages 27-41 in T. Nakashizuka and Y. Matsumoto, editors. Diversity and Interaction in a Temperate Forest Community: Ogawa Forest Reserve of Japan. Springer-Verlag, Tokyo.
- Suzuki, Y., M. Yui, and I. Date. 1991. Breeding bird community in the northernmost range of Japanese beech forests. *Strix* **10**:213-218 (in Japanese with English summary).
- Takeuchi, K. 2001. Nature conservation strategies for the “Satoyama” and “Satochi” , habitats for secondary nature in Japan. *Global Environmental Research* **5**:193-198.
- Takeuchi, K., R. D. Brown, I. Washitani, A. Tsunekawa, and M. Yokohari. 2003. Satoyama: The Traditional Rural Landscape of Japan. Springer, Tokyo.
- Tanaka, H., and T. Nakashizuka. 2002. Ground design of the research site. Pages 43-49 in T. Nakashizuka and Y. Matsumoto, editors. Diversity and Interaction in a Temperate Forest Community: Ogawa Forest Reserve of Japan. Springer-Verlag, Tokyo.
- ter Braak, C. F., and P. Šmilauer. 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, NY.
- Terborgh, J. 1989. *Where Have All the Birds Gone? : Essays on the Biology and Conservation of Birds that Migrate to the American Tropics*. Princeton University Press, Princeton, NJ.
- The Ornithological Society of Japan. 2000. Check-list of Japanese Birds, 6th Revised Edition. The Ornithological Society of Japan, Obihiro.
- The Ornithological Society of Japan. 2012. Check-list of Japanese Birds, 7th Revised Edition. The Ornithological Society of Japan, Sanda.
- Tojo, H. 1994. Population increase of the Red-billed *Leiothrix* *Leiothrix lutea* in the Massif

- Tsukuba. Japanese Journal of Ornithology **43**:39-42 (in Japanese with English summary).
- Tojo, H. 2007. Estimating species number of forest-dependent birds in Japan. Bulletin of FFPRI **6**:9-26 (in Japanese with English summary).
- Tojo, H., and S. Nakamura. 1999. Seeds found in fecal samples from Red-billed Leiothrix *Leiothrix lutea*. Japanese Journal of Ornithology **47**:115-117 (in Japanese with English summary).
- Tojo, H., K. Osawa, H. Terauchi, M. Kajita, A. Kajita, and O. Watanuki. 2004. Invasion by White-browed Laughing Thrushes (*Garrulax sannio*) into central Japan. Global Environmental Research **8**:23-28.
- Tomiałojć, L., and T. Wesołowski. 1990. Bird communities of the primaeval temperate forest of Białowieża, Poland. Pages 141-165 in A. Keast, editor. Biogeography and Ecology of Forest Bird Communities. SPB Academic Publishing bv, Hague.
- Totman, C. 1989. The Green Archipelago: Forestry in Preindustrial Japan. The University of California Press, Berkeley.
- Tsukada, M. 1982. *Cryptomeria japonica*: Glacial refugia and late-glacial and postglacial migration. Ecology **63**:1091-1105.
- Tsumura, Y., K. Uchiyama, Y. Moriguchi, S. Ueno, and T. Ihara-Ujino. 2012. Genome scanning for detecting adaptive genes along environmental gradients in the Japanese conifer, *Cryptomeria japonica*. Heredity **109**:349–360.
- Uchiyama, T. 2003. Vegetation history of Japanese cool-temperate and mid-temperate forest. Japanese Journal of Historical Botany **11**:61-71 (in Japanese with English summary).
- Ueuma, Y. 1979. Bird community in the upper part of river Sai-kawa and Mt. Takasaburo, Ishikawa Prefecture (2) Time of occurrence and seasonal change in number. Hakusan

- Nature Conservation Center, Ishikawa **5**:67-86 (in Japanese with English summary).
- Uramoto, M. 1961. Ecological study of the bird community of the broad-leaved deciduous forest of central Japan. *Journal of Yamashina Institute for Ornithology* **3**:1-32.
- Washitani, I. 2001. Traditional sustainable ecosystem 'Satoyama' and biodiversity crisis in Japan : conservation ecological perspective. *Global Environmental Research* **5**:119-133.
- Watari, Y., S. Nishijima, M. Fukasawa, F. Yamada, S. Abe, and T. Miyashita. 2013. Evaluating the "recovery level" of endangered species without prior information before alien invasion. *Ecology and Evolution* **3**:4711-4721.
- Wesołowski, T. 2007. Primeval conditions - what can we learn from them? *Ibis* **149**:64-77.
- Whelan, C. J., Ç. H. Şekercioğlu, and D. G. Wenny. 2015. Why birds matter: from economic ornithology to ecosystem services. *Journal of Ornithology* **156**:227-238.
- Williamson, K. 1964. Bird census work in woodland. *Bird Study* **11**:1-22.
- Yamagawa, H., S. Ito, K. Sakuta, N. Mizoue, and T. Nakao. 2009. Effects of small-scale clearcutting management on species diversity and vertical structure of understory vegetation of a conifer plantation comprising uneven-aged stands, in Kyushu, southern Japan. *Journal of the Japanese Forest Society* **91**:277-284 (in Japanese with English summary).
- Yamaura, Y. 2007. Mitigating effects of broadleaved forest fragmentation on birds: Proposal of plantation matrix management. *Journal of the Japanese Forest Society* **89**:416-430 (in Japanese with English summary).
- Yamaura, Y., S. Ikeno, M. Sano, K. Okabe, and K. Ozaki. 2009. Bird responses to broad-leaved forest patch area in a plantation landscape across seasons. *Biological Conservation* **142**:2155-2165.
- Yamaura, Y., K. Katoh, and T. Takahashi. 2006. Reversing habitat loss: deciduous habitat

- fragmentation matters to birds in a larch plantation matrix. *Ecography* **29**:827-834.
- Yamaura, Y., K. Katoh, and T. Takahashi. 2008. Effects of stand, landscape, and spatial variables on bird communities in larch plantations and deciduous forests in central Japan. *Canadian Journal of Forest Research* **38**:1223-1243.
- Yong, D. L., Y. Liu, B. W. Low, C. P. Españaola, and K. Kawakami. 2015. Migrant songbirds in the East Asian-Australasian Flyway: a review from a conservation perspective. *Bird Conservation International* **25**:1-37.
- Yui, M. 1976. The analyses of structure of the woodland bird community in Japan. I. Similarity, type classification and species composition of bird communities in breeding season. *Journal of Yamashina Institute for Ornithology* **8**:223-248 (in Japanese with English summary).
- Yui, M. 1977. Analyses of structure of the woodland bird community in Japan. II. Similarity, type classification and species composition of bird communities in winter. *Journal of Yamashina Institute for Ornithology* **9**:29-45 (in Japanese with English summary).
- Yui, M. 1983. Analyses of structure of the woodland bird community in Japan. III. Annual variation of breeding community. *Journal of Yamashina Institute for Ornithology* **15**:19-36 (in Japanese with English summary).
- Yui, M., and N. Ishii. 1994. Ringyo to Yasei-tyojyu no Kyouzon ni Mukete: -Shinrin Tyojyu no Seisoku-kankyō Hogo Kanri [Toward the Coexistence between Forestry and Wildlife: -Protection and Management of Habitat for Wildlife in Forests]. Nihon Ringyo Gijutu Kyokai, Tokyo (in Japanese).