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Differences in Bird Communities on the Forest Edge and in the Forest Interior: Are There Forest-interior Specialists in Japan?

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Abstract. Most North American bird species that are less successful in small forests than in large forests, are forest-interior specialists that winter in the tropics. These species have declined in small forests because of high rates of nest predation and brood parasitism near the forest edge. To determine whether migratory forest-interior specialists are also important components of bird communities in Japan, we surveyed bird populations on plots at the edge and in the interior of deciduous forests in Hokkaido and Kyoto. Surveys were conducted during the breeding season in forest fragments using the point count method. We calculated edge indices for the most abundant species in Hokkaido and Kyoto (38 and 18 species, respectively). Among the nine species that were more abundant in interior than in edge plots in Hokkaido were the following tropical migrants: *Turdus cardis, Phylloscopus coronatus*, and *Cuculus saturatus*. In Kyoto, the abundance of particular species of tropical migrants was too low to permit statistical analysis. We therefore analyzed the rare species as a group and this group was more abundant in the forest interior than on the forest edge. Three resident species, *Garrulus glandrius, Picus awokera*, and *Bambusicola thoracica*, were also more abundant in the forest interior. The most frequent potential nest predator, *Corvus macrorhynchos*, was more abundant at the edge than in the interior in Hokkaido, but showed the reverse pattern in Kyoto. The abundance of the most frequent brood parasite in Hokkaido, *Cuculus saturatus*, had a weak positive relation with the abundance of its host species, but was not significantly related to the distance from the forest edge. Therefore, the major negative edge effects in Japan may be due to nest predation by corvids. The impact of negative edge effects, as well as the effect of forest structure, on forest-interior birds in Japan should be the focus of future research.

Key words: Bird community, Forest fragmentation, Forest interior, Edge effect, Tropical migrant.
キーワード：鳥類群集，森林の分断化，林内種，林縁の危険性，熱帯への渡り鳥(夏鳥).

Introduction

The fragmentation of large forests into small, isolated patches is known to have negative effects on many species of animals. This phenomenon is especially well documented for birds in Europe and eastern North America, but has not been studied as intensively in Japanese forests. Deciduous forests in Japan are similar to those in Europe and eastern North America, with many of the same dominant genera of trees (e.g.,

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Quercus, Acer, Fagus). Also, Japanese forests have been subject to extensive clearing and fragmentation for agricultural, industrial and residential development, especially in lowland areas which have a long history of human settlement (Embree 1988). Consequently, only remnant patches of deciduous forests remain in Japan (Maeda 1993). Recent reports indicate that forest birds, especially tropical migrants, may be declining in many parts of Japan (Endo 1993, Morishita *et al.* 1997), and surveys of forests in the Tokyo region suggest that some species of birds may be less abundant in small, remnant patches of forest than in large forests (Higuchi *et al.* 1982). However, a conclusive analysis of the impact of habitat fragmentation on forest birds in Japan should begin by distinguishing forest-interior specialists from generalized woodland species and forest-edge specialists (Askins *et al.* 1987). If there are area-sensitive species that tend to disappear from small forests, they are most likely to be found among the forest-interior specialists.

In eastern North America many species of birds, especially tropical migrants (i.e., species that breed in the temperate region and migrate a long distance to the tropics) tend to decrease or disappear in small, isolated forests (Ambuel and Temple 1983, Askins *et al.* 1990). Also, the same species tend to occur more frequently in plots in large forests than in plots of the same size in small forests. Nearly all of these area-sensitive species are forest specialists that are primarily restricted to the forest interior. Similarly, most of the area-sensitive species in the deciduous forests of western Europe are forest-interior birds (Opdam *et al.* 1985) or mature-forest specialists that are not normally found in open habitats (Virkkala 1987). Thus, in both Europe and North America the species that are negatively affected by forest fragmentation are species that are largely restricted to the interior of large forests or mature forests.

In North America, forest-interior birds generally have lower reproductive rates in small forests because even the center of the forest is close to the forest edge. Nest predators, such as Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), raccoons (*Procyon lotor*), and feral and domestic cats (*Felis domesticus*) (Bider 1968, Askins *et al.* 1990, Donovan *et al.* 1997), and a brood parasite, the Brown-headed Cowbird (*Molothrus ater*) (Faaborg *et al.* 1995), tend to be more abundant near the forest edge than deep within the forest. The negative effects of these predators and parasites on nest success are most intense within 50 m of the forest edge (Paton 1994, Faaborg *et al.* 1995). Forest fragmentation also increases the rate of nest predation by corvids (particularly Hooded Crows, *Corvus cornix*) for forest songbirds in northwestern Europe (Møller 1989, Andrén 1992). Unless a large forest has a highly irregular shape, most of its area will be buffered from these negative edge effects, but in small forests the edge effects can have a major impact on the reproductive rates of forest-interior birds (Robinson 1992, Porneluzi *et al.* 1993).

Forest-interior specialists are generally more vulnerable to negative edge effects than more generalized species that are found in a wide range of habitats (including edge habitats). Many forest-interior species in North America build open-cup nests close to the ground and they only raise one brood per year, so they are particularly susceptible to the impact of terrestrial nest predators (Greenberg 1980, Whitcomb *et al.* 1981). Also, their populations cannot be sustained by immigration from surrounding disturbed habitats

because they are restricted to the forest. However, in contrast to the situation in North America, most bird species in European deciduous forests are generalists that also nest in other habitats, and there are few forest-interior specialists (McLellan *et al.* 1986, Lynch 1987). This may account for the lower number of area-sensitive species in European forests compared to similar forests in North America (Mönkönnen and Welsh, 1994).

When analyzing the effects of forest fragmentation on birds, it is important to focus on habitat specialists, such as forest-interior birds. If forest-edge specialists and generalized (interior/edge) species are included in the analysis, then the species richness in small forests may be equal to or greater than that in large forests (Whitcomb *et al.* 1981, Askins *et al.* 1987). The greater diversity of edge and generalized species in small forests with a high proportion of edge habitat may mask the loss of forest-dependent species.

The major goals of our study were to determine whether (1) some species of birds in Japan are largely restricted to the forest interior, and (2) whether crows and jays (Corvidae), which are important nest predators (Cramp 1994), and cuckoos (Cuculidae), which are brood parasites (Nakamura and Nakamura 1995), are more abundant near the forest edge than in the forest interior. In order to answer these questions, we compared standardized plots along the forest edge and in the forest interior in central Japan (Kyoto region) and in northern Japan (southern Hokkaido). The forests of Kyoto have been fragmented for centuries, while forest clearing primarily occurred since the late nineteenth century in Hokkaido (Totman 1989), so we were able to determine whether the diversity of forest-interior birds differs in two regions with different histories of forest disturbance.

Methods

We censused the birds in fragmented deciduous forests in central Japan (Kyoto: 35°N, 136°E) and northern Japan (southern Hokkaido: 43°N, 141°E) (Fig. 1). The study was conducted in the breeding season in 1988 in Kyoto, and in 1997 in Hokkaido. The climate in both regions is mild to cool and moist. Broad-leaved deciduous forests or mixed deciduous/coniferous forests in the lowlands were selected for the study sites because this type of forest has the richest avifauna (Fujimaki 1981, Kanai *et al.* 1996), and forest fragmentation has been well studied in this type of habitat in North America (Askins *et al.* 1990) and in Europe (Opdam *et al.* 1985). The forests in Kyoto belong to the *Rhododendron macrosepali-Pinetum densiflorae* community in which *Quercus* sp., *Castanopsis* sp., *Acer* sp. and *Pinus densiflora* are the dominant trees (Miyawaki and Okuda, 1990). The forests in Hokkaido belong to the *Tilia maximovicziana-Quercus mongolica* community in which the major tree species are *Quercus crispula, Acer mono* and other hardwoods.

The border of a forest is defined as any treeless belt more than 10 m in width with an open canopy or paved surface. Thus, roads, railroads, and powerline rights-of-way were considered forest boundaries as well as open space such as pastures, developed land, and bodies of water.

In each forest site we surveyed birds in two-four plots at different distances from the forest edge to determine whether some species are primarily found in the forest interior. The bird survey in Hokkaido was completed on plots at 0 m, 100 m, and 200 m from the

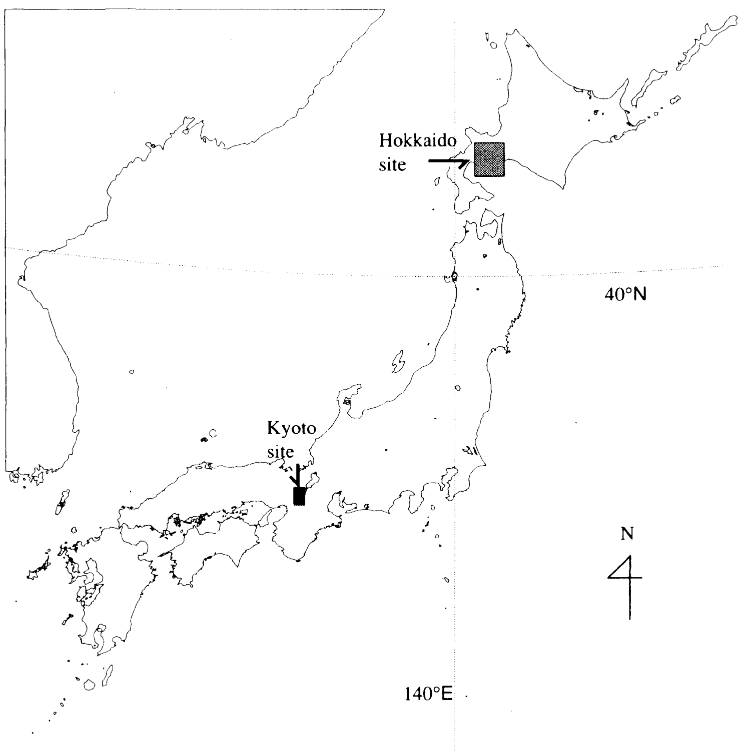

Fig. 1. Map of study sites in Hokkaido (▒) and Kyoto (■), Japan.

forest edge (34 sites), and also at 300 m (8 sites). In Kyoto, there were either one or two plots >100 m from the edge and a single plot on the edge at each of 19 sites.
The fixed-point count method was used for bird surveys because this method is suitable for efficiently sampling a large number of plots of uniform area (Whitcomb *et al.* 1981, Lynch and Whigham 1984, Askins *et al.* 1987). We visited each point twice, once during the early breeding season (Kyoto: April 11-May 15; Hokkaido: May 21 to June 7), and again in the late breeding season (Kyoto: May 16-June 13; Hokkaido: June 8 to June 20). The surveys were completed in the early morning when most birds are most active: between dawn (about 0400 hour) and 0830 in Hokkaido, and between 0630 and 0930 in Kyoto. Surveys were not completed when there was rain or high wind, or when loud noise occurred in the vicinity.

The abundance (number of individuals) of each species heard or seen was recorded during a 10-minute observation period at each survey point. All birds detected from the survey point were recorded for the Kyoto surveys, while only individuals within 50 m of the survey point were recorded at the Hokkaido sites. We counted more than one individual of a species only when they were seen or heard simultaneously, so the estimates of abundance are conservative. The abundance of each species was determined by the maximum number of individuals detected during the two visits except for summer

residents in Kyoto, where abundance was determined by the number of individuals detected during the late breeding season. Migrants were still passing through Kyoto during the early breeding season, so some of the summer residents detected at that time did not necessarily have breeding territories in the study plot.

An edge index was calculated to indicate the relative frequency of particular species on the forest edge and in the forest interior:

Edge Index (EI) = (average abundance at forest edge − average abundance in the interior)/(average abundance at forest edge + average abundance in the interior)

Values for this index range between −1.0 and +1.0. Forest interior species have negative EI values, indicating that they occur more frequently in the interior than at the edge, while edge species have positive EI values. An EI value close to 0 means that a species is equally abundant at the edge and in the interior. For Hokkaido data, average abundance of all plots at 100, 200, and 300 m were used for the interior average.

Species that occurred less than five times in a region and species that mainly use non-forested habitats such as bodies of water for foraging were excluded from the edge index calculation.

Abundance patterns were analyzed for potential brood parasites and nest predators, and for species with a total sample size of at least 15 observations. The analysis was conducted using analysis of variance and HSD tests for Hokkaido and the t-test for Kyoto, respectively.

We calculated the mean area of the sampled forests in the two regions to make certain that the results are not affected by the difference in forest sizes. The mean forest areas were 505 ha (SD 691) and 644 ha (SD 981) in Kyoto and Hokkaido, respectively, a difference which was not statistically significant ($t=0.94$, $df=50$, $P=0.35$). Therefore, we were comparing the abundance of birds at the edge and in the interior of forests of similar sizes in the two regions.

Results

In Hokkaido a total of 58 species was recorded in the survey plots (Appendix I). After excluding six species that forage outside the forests and 14 rare species, 38 species were used for the analysis (Table 1). A total of 29 species was recorded in Kyoto forests (Appendix I), 18 of which were used in the analysis (Table 2) except for four rare species indicated as "R" in Appendix I. There were no significant differences in number of species (species richness) (Hokkaido; $F=0.13$, $df=109$, $P>0.05$, Kyoto; $t=-1.53$, $df=36$, $P>0.05$), overall abundance (Hokkaido; $F=2.20$, $df=109$, $P>0.05$, Kyoto; $t=0.83$, $df=36$, $P>0.05$), or species diversity (Shannon-Weaver diversity index) (Hokkaido; $F=0.85$, $df=109$, $P>0.05$, Kyoto; $t=-0.64$, $df=36$, $P>0.05$) between the edge and the interior of forests in either region.

Habitat groups

Using the Edge Index, we categorized forest bird species into three major habitat

Table 1. Habitat types of forest birds in Hokkaido calculated and grouped by edge index. Edge index =(Average abundance at the edge-average abundance in the interior)/(average abundance at the edge+average abundance in all the interior). Results of analyses of the average abundance (number of individuals/plot) at each distance from the forest edge are shown (ANOVA). ___ and ___were significantly different in HSD; significance levels: *=$P<0.05$, **=$P<0.01$, ***=$P<0.001$. I=species more abundant in the interior, E=species more abundant at the edge, NS=Not significant, —=species excluded from pattern analysis due to insufficient sample sizes (n<15). (a)=does not breed in Kyoto. English names follow Brazil (1991), and see Appendix I for scientific names.

Habitat group	English name	Mean Abundance (0m)	(100m)	(200m)	(300m)	$F(df=106)$	P	Results	Edge Index
	Goldcrest	0.00	0.06	0.13	0.00			—	−1.00
	Japanese Green Pigeon	0.00	0.06	0.29	0.25	2.80	0.04	I*	−1.00
Forest	Varied Tit	0.03	0.21	0.10	0.31			—	−0.75
	Japanese White-eye	0.03	0.09	0.27	0.00			—	−0.60
Interior	Great Spotted Woodpecker	0.06	0.19	0.12	0.13			—	−0.44
	Gray Thrush	0.37	0.46	0.60	1.44	4.73	<0.01	I**	−0.38
	Coal Tit	0.18	0.41	0.47	0.31	1.58	0.20	NS	−0.38
	Eastern Crowned Warbler	0.47	0.85	1.10	1.19	3.25	0.03	I*	−0.38
	Oriental Cuckoo	0.13	0.29	0.38	0.13	1.87	0.14	NS	−0.35
	Eurasian Jay	0.09	0.15	0.16	0.19	0.20	0.90	NS	−0.30
	Japanese Grosbeak	0.25	0.32	0.35	0.63	0.85	0.47	NS	−0.29
	Arctic Warbler	0.21	0.32	0.27	0.50	0.84	0.47	NS	−0.27
	Narcissus Flycatcher	0.50	0.79	0.79	0.94	1.20	0.31	NS	−0.25
	Siberian Blue Robin	0.16	0.37	0.32	0.13	1.19	0.32	NS	−0.25
	Short-tailed Bush Warbler	0.49	0.74	0.78	0.88	1.78	0.16	NS	−0.24
	Marsh Tit (a)	0.49	0.56	0.78	0.81	0.95	0.42	NS	−0.20
Forest	Brown Flycatcher	0.12	0.15	0.12	0.25	0.16	0.92	NS	−0.18
	Japanese Pygmy Woodpecker	0.28	0.24	0.28	0.56	0.86	0.47	NS	−0.13
	Blue-and-white Flycatcher	0.28	0.35	0.40	0.25	0.36	0.78	NS	−0.10
Gener-	Bush Warbler	0.60	0.62	0.79	0.56	0.53	0.66	NS	−0.05
alist	Russet Sparrow	0.34	0.31	0.28	0.38	0.06	0.98	NS	0.03
	Pale-legged Warbler	0.09	0.06	0.06	0.13			—	0.05
	Rufous Turtle Dove	0.37	0.26	0.34	0.38	0.19	0.90	NS	0.05
	Brown-eared Bulbul	1.26	1.37	0.99	1.00	1.04	0.38	NS	0.06
	Long-tailed Tit	0.18	0.13	0.18	0.13	0.06	0.98	NS	0.10
	Black-faced Bunting (a)	1.34	1.10	1.22	0.88	0.72	0.54	NS	0.11
	Great Tit	1.09	0.74	0.65	1.13	2.58	0.06	NS	0.14
	White-backed Woodpecker	0.12	0.06	0.07	0.13			—	0.16
	Brown Thrush	0.34	0.32	0.15	0.13	0.96	0.41	NS	0.27
	Olive-backed Pipit	0.09	0.03	0.10	0.00			—	0.34
	Long-tailed Rosefinch (a)	0.15	0.09	0.06	0.00			—	0.51
Forest	Oriental Greenfinch	1.02	0.60	0.27	0.06	8.29	<0.01	E***	0.54
	Carrion Crow	0.21	0.00	0.18	0.00			—	0.56
Edge	Red-cheeked Starling (a)	0.43	0.18	0.06	0.13	1.82	0.15	NS	0.57
	Jungle Crow	1.62	0.65	0.40	0.06	4.23	<0.01	E**	0.63
	Siberian Meadow Bunting	0.37	0.00	0.00	0.00			—	1.00
	Black-backed Wagtail (a)	0.21	0.00	0.00	0.00			—	1.00
	Eurasian Tree Sparrow	0.94	0.00	0.00	0.00	5.58	<0.01	E***	1.00

Table 2. Habitat types of forest birds in Kyoto calculated and grouped by edge index (see Table 1). Results of analyses of the average abundance (number of individuals/plot) at the edge and the average abundance in the interior are shown (t-tests). I=species more abundant in the interior, E=species more abundant at the edge, NS=Not significant, —=species excluded from pattern analysis due to insufficient sample sizes (n<15). Significance levels: $*=P<0.05$, $**=P<0.01$. (b)=does not breed in Hokkaido. English names follow Brazil (1991), and see Appendix I for scientific names.

Habitat group	English name	Mean Abundance		t (df=36)	P	Results	Edge Index
		Edge	Interior				
Forest Interior	Eurasian Jay					—	−1.00
	Japanese Green Woodpecker (b)					—	−0.69
	Bamboo Partridge (b)					—	−0.40
Forest Generalist	Varied Tit	0.58	0.92	−1.81	0.08	NS	−0.23
	Siberian Meadow Bunting	0.53	0.82	−1.52	0.14	NS	−0.21
	Bush Warbler	0.37	0.55	−0.75	0.46	NS	−0.20
	Jungle Crow	1.21	1.68	−2.45	0.02	I*	−0.16
	Great Tit	1.26	1.55	−1.19	0.24	NS	−0.10
	Long-tailed Tit	0.42	0.47	−0.34	0.74	NS	−0.05
	Japanese White-eye	1.05	1.13	−0.43	0.67	NS	−0.04
	Brown-eared Bulbul	2.53	2.24	1.44	0.16	NS	0.06
	Japanese Grosbeak	0.47	0.37	0.50	0.62	NS	0.15
	Carrion Crow	0.63	0.37	1.64	0.11	NS	0.26
	Japanese Pygmy Woodpecker	0.63	0.34	1.96	0.07	NS	0.30
Forest Edge	Rufous Turtle Dove	0.89	0.39	2.24	0.03	E*	0.39
	Green Pheasant					—	0.48
	Oriental Greenfinch					—	0.48
	Eurasian Tree Sparrow	0.79	0.03	3.60	<0.01	E**	0.92

groups: the forest interior ($-1 \leq EI \leq -0.34$), generalist ($-0.34 < EI < 0.34$), and edge ($0.34 \leq EI \leq 1$) groups (Tables 1 and 2). In Hokkaido, both the forest interior and the edge groups had nine species, whereas the generalist group had 20 species. There were five species which breed only in northern Japan and did not breed in the Kyoto region (Table 1). In Kyoto, there were three species in the forest interior group, four species in the edge group, and 11 species in the generalist group (Table 2). Two of the species which breed in Kyoto region did not breed in Hokkaido. Species classified in the same category in both regions were Oriental Greenfinch and Tree Sparrow, both of which were in the edge group.

The overall rank order of the edge index values of 15 species found in both Hokkaido and Kyoto was similar in the two regions (Wilcoxon signed rank test, $t=-10.00$, $df=14$, $P=0.60$). However, there is a tendency for particular species to be more generalized in their use of interior or edge habitats in Kyoto than in Hokkaido (Fig. 2). Many of the species classified as forest-interior or edge specialists in Hokkaido were classified as generalists in Kyoto (e.g. Japanese White-eye, Varied Tit, Jungle Crow and Siberian Meadow Bunting). The species that were more generalized in Kyoto tended to be more abundant there than in Hokkaido; this was true for Japanese White-eye, Varied Tit, and

Siberian Meadow Bunting for both forest edge and forest interior plots, and for Jungle Crow for interior plots (Tables 1 and 2). Brown-eared Bulbul was also more abundant at both edge and interior plots in Kyoto than in Hokkaido, but it was classified as a generalist in both regions.

Distribution pattern at the edge and in the interior of forests

In order to determine whether the patterns described by the edge index are confirmed statistically, we analyzed the distribution of 27 species (all species with $\geq$ 15 observations) in Hokkaido (Table 1). In the forest-interior group, Japanese Green Pigeon, Gray Thrush, and Eastern Crowned Warbler were significantly more abundant in the inner forest ($P<0.05$). However, Coal Tit and Oriental Cuckoo did not have significant patterns. Among the edge species, Oriental Greenfinch, Jungle Crow and Tree Sparrow were significantly more abundant at the forest edge. As expected, no species in the generalist group (those species with low edge index values) showed significant patterns with respect to distance from the edge.

In Kyoto, the forest interior species were not frequent enough at survey points to permit analysis of individual species, but we compared the abundant species in the generalist (11) and the edge (2) groups (Table 2). Within the generalist group, only Jungle Crow showed a significant difference between the edge and interior (Table 2). Jungle Crows were more abundant in the interior than at the edge. Rufous Turtle Doves were significantly more abundant at the edge, showing the opposite distribution from Jungle Crow. This pattern was different from the pattern in Hokkaido, where Jungle Crow was in the edge group and significantly more abundant at the edge, and Rufous Turtle Dove was in the generalist group. Eurasian Tree Sparrow was classified as an edge specialist and was significantly more abundant on the edge than in the interior in both regions.

There were eleven species in Kyoto which we did not categorize into habitat groups because of insufficient sample sizes (Appendix I). However, rare species are often species of conservation concern (Askins *et al.* 1987). We therefore analyzed the distribution in Kyoto of those rare species that were frequent enough in Hokkaido to be classified into habitat categories. Four of the rare species in Kyoto (Japanese Green Pigeon, Coal Tit, Eastern Crowned Warbler, and Oriental Cuckoo) were categorized in the forest-interior group in Hokkaido (Table 1). When considered as a group, the abundance of these four species was significantly higher in the forest interior than on the forest edge in Kyoto ($t = -3.75$, $df=36$, $P<0.01$), indicating that they show the same preference for forest interior habitat in Kyoto as in Hokkaido.

Negative edge effects

The largest difference between forest interior and edge in the two regions was in the distribution of corvids, which are potential nest predators. Jungle Crow abundance was greater at the edge than in the interior in Hokkaido, but the opposite was true in Kyoto.

The most abundant corvid in Hokkaido was the Jungle Crow. The numbers of this species roughly decreased with distance from the edge (Fig. 3). Since crows are known to

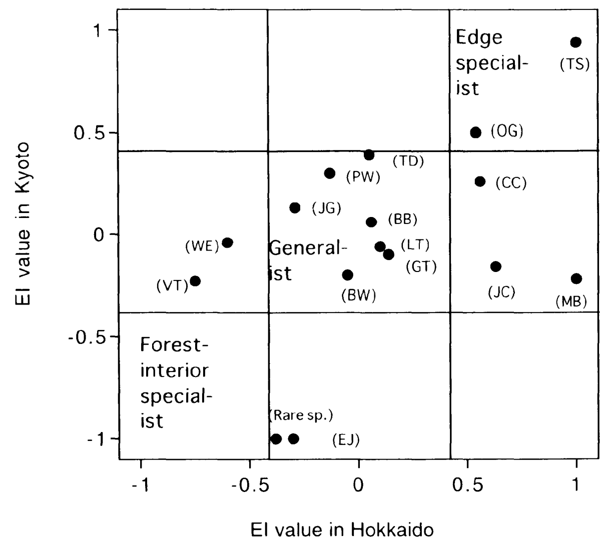

Fig. 2. Comparison of Edge Index values in Hokkaido and Kyoto.
Key to abbreviations: TS = Tree Sparrow, OG = Oriental Greenfinch, CC = Carrion Crow, MB = Siberian Meadow Bunting, JC = Jungle Crow, TD = Rufous Turtle Dove, PW = Japanese Pygmy Woodpecker, BB = Brown-eared Bulbul, JG = Japanese Grosbeak, LT = Longtailed Tit, GT = Great Tit, BW = Bush Warbler, WE = Japanese White-eye, VT = Varied Tit, EJ = Eurasian Jay, Rare sp. = Rare species group including Japanese Green Pigeon, Eastern Crowned Warbler, Coal Tit and Oriental Cuckoo.

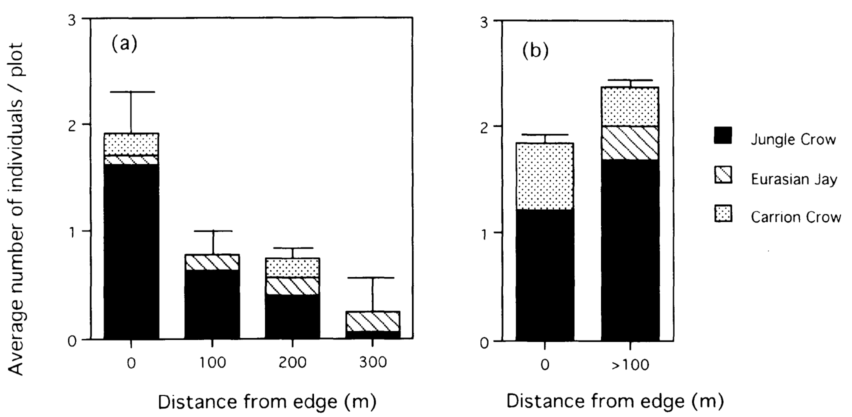

Fig. 3. Average abundance (number of individuals/plot) of corvids at different distances from the forest edge. (a) Hokkaido and (b) Kyoto. (Bar = SE). For scientific names, see Appendix I.

gather at roosts or foraging sites, we tested whether the abundance pattern of Jungle Crows was affected by large roosting or feeding aggregations (Kuroda 1990). When we excluded three sites which had exceptionally high crow abundance, the abundance of Jungle Crows was still significantly greater at the edge ($F_{(3, 97)} = 4.16$, $P = 0.01$). In

contrast, the abundance of Jays did not differ significantly for edge and interior points ($F_{(3, 106)}=0.20$, $P=0.90$). Carrion Crows were not common in the study sites and occurred only at the edge and at points 200 m from the edge. In general, corvids in Hokkaido were not limited to the forest edge, and penetrated into the forest at least as far as 300 m, but their overall abundance was highest near the edge and decreased significantly at points 200 m inside the forest.

In Kyoto, similarly, Jungle Crows were the most abundant corvids in the forest. However, they were significantly more abundant in the inner forest than at the edge ($t=-2.45$, $df=36$, $P=0.02$). Carrion Crows, which are usually associated with open country or agricultural land (Higuchi 1979, Arita 1988), did not show a statistically significant difference in abundance at the edge and interior in Kyoto ($t=1.64$, $df=36$, $P=0.11$). Jays were not abundant and occurred only in the forest interior. The tendency of higher corvid abundance in the forest interior in Kyoto was due to Jungle Crows and Jays, which occurred more abundantly in the forest interior than at the edge, more than compensating for the non-significant decrease of Carrion Crows in the interior.

Three species of brood parasites, namely Oriental Cuckoo, Hodgson's Hawk Cuckoo and Common Cuckoo, were recorded in Hokkaido (Appendix 1). The abundance of Oriental Cuckoo, the most common cuckoo species in the forest, was not related to distance from the edFe of the forest ($E_{(3, 106)}=1.87$, $P=0.14$). In contrast, Common Cuckoos were observed only at the edge or outside the forest, and Hodgson's Hawk Cuckoos were recorded only near the forest edge (0 and 100 m points). However, the abundance of Oriental Cuckoos showed a weak but significant positive relationship with the abundance of its host species (simple linear regression $r^2=0.09$, $F_{(1, 109)}=10.43$, $P<0.01$). The host species of Oriental Cuckoo recorded in Hokkaido and included in this analysis were Eastern Crowned Warbler, Siberian Blue Robin, Narcissus Flycatcher, Blue-and-white Flycatcher and Bush Warbler (Nakamura and Nakamura 1995, Higuchi 1996). The abundance of this cuckoo showed no statistically significant relationship with the abundance of non-host species ($r^2=0.04$, $F_{(1, 109)}=4.04$, $P=0.05$), suggesting that the Oriental Cuckoo, the most common brood parasite in the forest, is distributed where its breeding resources are abundant (Higuchi and Sato 1984).

In Kyoto, cuckoos were rare and only one Oriental Cuckoo was recorded during the study.

Discussion

Habitat groups

We categorized species into habitat groups (forest-interior, generalist and edge) using the edge index, which is a measure of difference in average abundance between the edge and the interior. The abundance of some species in the forest-interior group increased significantly with distance from the edge to the forest interior, indicating that they are concentrated in the forest interior in Japan. Moreover, when species that were rare in Kyoto and were classified as forest-interior species in Hokkaido were considered as a rare species group, the overall abundance of this group was significantly higher in the forest

interior than at the forest edge, indicating that their distributional patterns are similar in the two regions.

There was no significant difference in the overall abundance, species richness, or species diversity of birds at the edge and the interior of forests. This does not necessary mean, however, that forest edges do not have a negative impact on forest bird populations. In North America, forest-interior species are less tolerant of forest fragmentation than forest generalists because the core area of interior forest they need for successful nesting is reduced or lost (Askins *et al.* 1990). Thus, specific habitat requirements have substantial implications for conserving particular species. The forest generalists and the edge species may not be affected by forest fragmentation in the same way as interior species. Also both groups of habitat specialists, the forest-interior species and the edge species, are less numerous than forest generalists in the two study regions. Therefore, the different distributions of species and the differences in species composition in the forest interior are obscured if only overall trends for all species of birds are analyzed.

Life history traits of forest-interior species

The most striking difference between the two regions was in the abundance of tropical migrants. In Hokkaido, 11 of 38 species were tropical migrants, and many other species migrate a short distance to southern Japan in winter. Except for Red-cheeked Starlings, all of the tropical migrants had negative edge index values. Among the tropical migrants in Hokkaido, Gray Thrushes, Eastern Crowned Warblers and Oriental Cuckoos are in the forest interior group, and, except for the brood-parasitic Oriental Cuckoos, they nest very low, either on the ground or in shrubs or low trees (Nakamura and Nakamura 1995). These life history traits are also found in many North American forest-interior species that are area-sensitive (i.e., less abundant in small forests; Whitcomb *et al.* 1981, Askins *et al.* 1987). Although their nests are vulnerable to terrestrial predators, they may suffer less predation deep within the interior of forests if the predators primarily come from outside of the forest or from the forest edge (Paton 1994).

In contrast, all species analyzed in Kyoto were residents, and the tropical migrants were rare. Considering that the rare tropical migrants in Kyoto are also probably forest-interior specialists, they may be vulnerable to forest fragmentation. As a result, they may have already declined as a result of a long history of forest fragmentation near Kyoto.

Although the relatively small number of forest-interior birds in Kyoto is not due to more severe fragmentation of the study sites, it may be due to differences in the history of forests in Kyoto and Hokkaido. Deciduous forests in North America have more species of forest-interior specialitsts than similar forests in Europe, and several researchers have hypothesized that this may result from the longer history of forest fragmentation due to land clearing in Europe (Ford 1987, McLellan *et al.* 1986, Mönkkönen and Welsh 1994). The forests in Kyoto region have been fragmented for centuries, while those of Hokkaido have only been extensively fragmented for less than a hundred years. Although the rank order of edge index values was not different for species found in both Hokkaido and Kyoto, there was a tendency for Kyoto populations to be more generalized than populations of the same species in Hokkaido. The birds of Kyoto and other lowland areas of

Honshu may have had more time to adapt to forest fragmentation, becoming more generalized in their habitat preferences. This type of behavioral or evolutionary change may have occurred in European populations of the Winter Wren, which is a forest specialist in Poland and Finland, but is a habitat generalist in England, where there is a longer history of forest clearing (Ford 1987). Those species that could not adapt to forest fragmentation in Kyoto may have disappeared from the region.

Another possibility is that the forests in Kyoto are less mature than those in Hokkaido because of a long and continual history of coppice use that only ended recently. If the forests in Kyoto are less mature or productive than those in Hokkaido, then they may provide fewer niches for habitat specialists. These two factors of fragmentation and maturity of forests are not mutually exclusive, however. To clarify these points, further studies are needed on the relation between bird species composition and forest structure and history in different regions of Japan.

The bird species vulnerable to forest fragmentation in Japan were not limited to the tropical migrant group as was found in eastern North America, but include species with various other life history traits. Traits other than tropical migration shared by some forest-interior species were medium to large body size, specific foraging behavior such as fruigivory or carnivory, and requirement for large, old trees. Larger species require a larger territory or home range for their food and breeding requirements (Kattan *et al.* 1994), so they are prone to suffer from habitat fragmentation. Species that depend on specific habitats are vulnerable to habitat fragmentation because the specific habitat may be lost when the surrounding environment is changed. Large cavity nesters are particularly vulnerable when forests are fragmented because large or old trees are susceptible to increased wind exposure. Species with more than one of these vulnerable traits will be of special concern when their habitat is fragmented; these include Japanese Green Pigeon, Great Spotted Woodpecker, Japanese Green Woodpecker (an endemic species to southern Japan), Bamboo Partridge and Eurasian Jay. Red-cheeked Starling, although an edge specialist, is a tropical migrant that breeds only in northern Japan. This nearly endemic, cavity-nester may also require special attention.

Negative edge effects

Of the two potential negative edge effects we considered, nest predation by corvids was potentially the more important for forest birds in Japan because of the abundance of crows. The distribution of Jungle Crows, the most abundant corvid in both regions, showed different patterns in the two study regions. In Hokkaido, Jungle Crows were more abundant at the edge than in the interior, whereas in Kyoto, they were more abundant in the interior than at the edge. This is consistent with recent results from the midwestern United States that indicate that negative edge effects caused by predators and brood parasites show major regional differences that are related to the amount and distribution of forest across the regional landscape (Donovan *et al.* 1997). Our results suggest that nest predation may potentially create a strong negative edge effect in Hokkaido because crows are concentrated along the forest edge and there are few crows in the forest interior. In contrast, the density of crows was significantly greater in the forest interior than along

the forest edge in Kyoto, suggesting that songbirds are not protected from these predators if they nest in the forest interior. Perhaps this is one reason that forest-interior birds are infrequent in these forests compared to the forests in Hokkaido. It is unclear why Jungle Crows (the most abundant species of crow) show such a different distributional pattern in the two regions. This species thrives in cities, but prefers to nest at sites away from human activity (Karasawa 1989), so the large population in the city of Kyoto may use nearby forests for nesting. In Hokkaido, where the human population is less dense, crows may be able to nest in areas outside of the forest. It is necessary to study the habitat preference of Jungle Crows in various regions of Japan to further clarify this inconsistency. Populations of Jungle Crows have recently grown in larger cities (Kawasawa *et al.* 1991), which increases the threat to nesting birds, especially those with open-cup, tree-top nests. Super-abundant crow populations could be controlled by reducing access to artificial food sources such as garbage.

Brood parasites occurred in all of the forest habitats in Hokkaido. Because the Oriental Cuckoo is a specialized forest cuckoo and was associated with its host species (Higuchi 1996), the host species in Hokkaido will not be able to avoid parasitism by avoiding the forest edge. Consequently, behavioral defense mechanisms, such as nest defense, egg detection and egg rejection, may be more important than nest location for preventing parasitism (Takasu *et al.* 1993). Oriental Cuckoos are tropical migrants, and like other tropical migrants, they were rare in Kyoto. However, cuculids are adaptable enough to parasitize new host species (Higuchi 1996, Takasu *et al.* 1993, Nakamura and Kashiwagi 1995). As the forest becomes increasingly fragmented, the probabiliy that a forest-interior species will encounter a new cuckoo species increases, so the impact of brood parasitism on forest birds should be monitored.

We excluded rare species from statistical analysis because of insufficient sample sizes. However, many of the rare species have traits that are often associated with sensitivity to forest fragmentation, such as tropical migration, moderately large body size, and frugivory. Eastern Crowned Warblers and Oriental Cuckoos, both of which are tropical migrants, were forest-interior species in Hokkaido. Japanese Green Pigeon, a large fruigivorous species, was a forest-interior species which was absent at the edge in Hokkaido. The rarity of these species in Kyoto, along with the declining trends of tropical migrants in many areas of Japan, indicate that migratory forest birds should be studied more intensively in Japan (Endo 1993, Morishita *et al.* 1997). This research should especially focus on forest-interior species.

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林縁と林内の鳥類群集の違い：日本に林内種はいるか？

森林の分断化に伴い，北米では森林の奥で繁殖し，熱帯地方に渡って越冬する種に繁殖成功率の低下が目立つ。林縁では巣の捕食と托卵が多く，分断化されて奥が浅くなった森林ではこれらの危険性が内部まで及ぶからである。日本の鳥類群集にもこのような林内だけに適応した鳥種がいるかどうかを明らかにするために，北日本（北海道）と中部（京都）の落葉広葉樹林の林縁と林内で鳥類の種数と密度の調査を行なった。分断化された森林で繁殖期に定点調査を行なった。見られた鳥のうちで数が多いものについて林縁指数を計算した（北海道；38 種，京都；18 種）。北海道で林縁より林内に多かった種に熱帯に渡る夏鳥のクロツグミ (*Turdus cardis*)，センダイムシクイ (*Phylloscopus coronatus*)，ツツドリ (*Cuculus saturatus*) がいた。京都では熱帯に渡る夏鳥の個体数は少なすぎて，林縁指数を計算できなかったため，解析には「希少種」としてまとめたグループに入れた。林内に個体数が多かったのは，アオバト (*Sphenurus sieboldii*) を含んだ「希少種グループ」と，留鳥であるカケス (*Garrulus glandarius*)，アオゲラ (*Picus awokera*)，コジュケイ (*Bambusicola thoracica*) がいた。

巣の捕食をする可能性のある鳥で一番数が多かったのはハシブトガラス (*Corvus macrorhynchos*) で，北海道では林縁に，京都では反対に林内に多かった。北海道の森林で一番多い托卵鳥はツツドリだったが，林縁からの距離との有意な相関関係はみられず，托卵の寄主の分布と弱いが有意な相関が見られた。北米と異なって，日本の林縁で多いのはカラス類による巣の捕食の危険性であると考えられる。今後は林内種に対する林縁の危険性に焦点を当てた研究が必要である。

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Appendix 1. Bird species recorded in this study. A = excluded from analyses because non-forest specialist, B = excluded because occurred only outside of forests, C = excluded due to insufficient sample sizes, D = does not breed in the region, R = analyzed as rare species, — = was not recorded in this region. English names follow Brazil (1991) and scientific names follow Ornithological Society of Japan (1997).

English name	Scientific name	Hokkaido	Kyoto	English name	Scientific name	Hokkaido	Kyoto
Sparrow Hawk	*Accipiter nisus*	C	—	Arctic Warbler	*Phylloscopus borealis*		D
Woodcock	*Scolopax rusticola*	C	—	Eastern Crowned Warbler	*Phylloscopus coronatus*		R
Green Pheasant	*Phasianus colchicus*	—		Pale-legged Warbler	*Phylloscopus tenellipes*		—
Bamboo Partridge	*Bambusicola thoracica*	D		Goldcrest	*Regulus regulus*		—
Japanese Green Pigeon	*Sphenurus sieboldii*		R	Blue-and-white Flycatcher	*Cyanoptila cyanomelana*		C
Rufous Turtle Dove	*Streptopelia orientalis*			Narcissus Flycatcher	*Ficedula narcissina*		C
Common Cuckoo	*Cuculus canorus*	C	—	Brown Flycatcher	*Muscicapa dauurica*		—
Hodgson's Hawk Cuckoo	*Cuculus fugax*	C	—	Sooty Flycatcher	*Muscicapa sibirica*	C	—
Oriental Cuckoo	*Cuculus saturatus*		R	Long-tailed Tit	*Aegithalos caudatus*		
Japanese Pygmy Woodpecker	*Dendrocopos kizuki*			Coal Tit	*Parus ater*		R
White-backed Woodpecker	*Dendrocopos leucotos*		—	Great Tit	*Parus major*		
Great Spotted Woodpecker	*Dendrocopos major*		—	Willow Tit	*Parus montanus*	C	—
Black Woodpecker	*Dryocopus martius*	C	D	Marsh Tit	*Parus palustris*		D
Gray-headed woodpecker	*Picus canus*	B	D	Varied Tit	*Parus varius*		
Japanese Green Woodpecker	*Picus awokera*	D		Nuthatch	*Sitta europaea*	C	—
Olive-backed Pipit	*Anthus hodgsoni*		—	Treecreeper	*Certhia familiaris*	C	—
Gray Wagtail	*Motacilla cinerea*	A	C	Japanese White-eye	*Zosterops japonica*		
Black-backed Wagtail	*Motacilla alba*		D	Siberian Meadow Bunting	*Emberiza cioides*		
Japanese Wagtail	*Motacilla grandis*	—	C	Black-faced Bunting	*Emberiza spodocephala*		—
Brown-eared Bulbul	*Hypsipetes amaurotis*			Gray Bunting	*Emberiza variabilis*	C	—
Bull-headed Shrike	*Lanius bucephalus*	A	C	Oriental Greenfinch	*Carduelis sinica*		
Winter Wren	*Troglodytes troglodytes*	C	—	Hawfinch	*Coccothraustes coccothraustes*	C	D
Gray Thrush	*Turdus cardis*		—	Japanese Grosbeak	*Eophona personata*		
Brown Thrush	*Turdus chrysolaus*		—	Long-tailed Rosefinch	*Uragus sibiricus*		D
Siberian Thrush	*Turdus sibiricus*	C	—	Eurasian Tree Sparrow	*Passer montanus*		
White's Thrush	*Zoothera dauma*	C	—	Russet Sparrow	*Passer rutilans*		—
Siberian Blue Robin	*Luscinia cyane*		—	Gray Starling	*Sturnus cineraceus*	A	C
Black-browed Reed Warbler	*Acrocephalus bistrigiceps*	A	—	Red-cheeked Starling	*Sturnus philippensis*		D
Bush Warbler	*Cettia diphone*			Eurasian Jay	*Garrulus glandarius*		
Short-tailed Bush Warbler	*Urosphena squameiceps*		C	Carrion Crow	*Corvus corone*		
Gray's Grasshopper Warbler	*Locustella fasciolata*	A	D	Jungle Crow	*Corvus macrorhynchos*		