Title	Effect of forest shape on habitat selection of birds in a plantation-dominant landscape across seasons: comparison between continuous and strip forests
Author(s)	Naoe, Shoji; Sakai, Shoko; Masaki, Takashi
Citation	Journal of Forest Research (2012), 17(2): 219-223
Issue Date	2012-04
URL	http://hdl.handle.net/2433/154868
Right	The final publication is available at www.springerlink.com
Type	Journal Article
Textversion	author

Effect of forest shape on habitat selection of birds in a plantation-dominant landscape across seasons: comparison between continuous and strip forests

Shoji NAOE[a*], *Shoko SAKAI*[b], *Takashi MASAKI*[c]

[a]*Center for Ecological Research, Kyoto University, Hirano 2–509–3, Otsu, Shiga 520–2113, Japan*

[b]*Research Institute for Humanity and Nature, Motoyama 457–4, Kamigamo, Kita-ku, Kyoto 603–8047, Japan*

[c]*Forestry and Forest Products Research Institute, Matsunosato 1, Tsukuba, Ibaraki 305–8687, Japan*

[*]*Corresponding author*: *Tel.*: +81 77 549 8019; *Fax*: +81 77 549 8201

E-mail address: shoji-n@ecology.kyoto-u.ac.jp

Article type: Short communication

Subject area: Biology and ecology

Field: Wildlife

Page count for the text: 16 pages

Numbers of tables and figures: 1 table and 2 figures

Abstract

Conversion of natural forests to other land use results not only in a decrease of forest area, but also in the degradation of remnant forests as a habitat for forest animals. Although such degradation due to an increase of forest edges has been studied most intensively, other factors such as forest shape may also contribute to the degradation. In this study, we compared bird abundance and species richness between irregular-shaped and relatively continuous forests in the breeding and migratory seasons. Since the forests were surrounded by tree plantations rather than open lands, the edge effect may have been weak at the study site. Our results suggested that the irregular forest shape negatively affected forest bird abundance and species richness in the breeding season, but not in the migratory season. The response of birds varied with bird traits: migrants avoided the irregular-shaped forest, but residents did not. Among the residents, small ones preferred or tolerate the irregular shaped forest whereas large ones avoided it. This study indicates that careful consideration of various factors such as seasonality and bird traits is needed to understand the consequences of land use changes on forest birds.

Keywords:

Plantation-dominant landscape; Migration habit; Forest shape; Seasonality; Forest bird

1. Introduction

Conversion of natural forests to other land use has become a major threat to forest animals. It results not only in a decrease of forest area, but also in the degradation of remnant forests that are habitat for forest animals. For example, partial deforestation frequently creates irregular-shaped forests (i.e., fragmented or strip-shaped) (e.g., Ranta et al. 1998). One of the important problems of such irregular-shaped forests is the high ratio of edge to forest area. Forest edges are usually very different from forest interiors with respect to abiotic and biotic conditions, and are not suitable habitat for many forest animals (Murcia, 1995). Such an edge effect is more pronounced when the forest is surrounded by open lands such as agricultural fields. The edge effect was first demonstrated as different composition of plants between edges and interiors, and it has been studied intensively in both plants and animals. To date, various examples of the edge effect have been demonstrated for a wide range of forest organisms (Ries et al., 2004). For forest birds, the major threat of the edge is predation or brood parasitism. Gates and Gysel (1978) demonstrated high predation loss (40-50 %) and brood parasitism loss (15-25 %) of forest birds' eggs or nestlings near the forest edge in remnant forests surrounded by open lands.

On the other hand, in remnant forests surrounded by plantations of woody plants, the edge effect is considered to be negligible, or at least much weaker. However, other negative effects of an irregular forest shape on forest animals are still conceivable. For example, forest animals might not be able to efficiently find foods or other resources in an irregular-shaped forest in which they can not maintain their optimally shaped home range for finding resources (See Recher et al., 1987). However, the effects of forest shape other than the edge effect have not been well studied (but see Lindenmayer et al., 2002).

In this study, we evaluated the effect of forest shape on forest birds by comparing highly irregularly shaped and more-or-less continuous forests in a plantation-dominant landscape in Japan. Although in forests surrounded by plantations the edge effect may be weak, the irregular shape may make foraging of birds less efficient. We monitored the birds in both the breeding and migratory seasons, since recent studies have suggested that habitat use of forest birds in a forest mosaic with strong anthropogenic activities differs between seasons (Keller and Yahner 2007; Keller et al. 2009; Yamaura et al. 2009; Naoe et al. 2011; but see Murgui 2007). We also evaluated whether the response of the birds differed depending on bird traits (bird migratory class and body weight), since many studies have demonstrated that the response of forest birds to vegetation changes differ with their traits (e.g., Keller et al., 2009).

2. Methods

2.1. Study sites

This study was conducted in the southern part of the Abukuma Mountains, Honshu (central Japan; 36°56’N, 140°35’E, 610–660 m a.s.l.). The annual precipitation is approximately 1910 mm, and mean annual temperature is 10.7°C, with average monthly temperatures ranging from -0.9°C in January to 22.6°C in August, based on data from a meteorological station in Ogawa (36°54’N, 140°35’E) (Moriguchi et al., 2002). The maximum snow depth in winter is about 50 cm.

We surveyed the species composition and density of forest birds in two forests: the relatively continuous Ogawa Forest Reserve (OFR; ca. 98 ha) and strip-shaped forest fragments nearby (FRG; ca. 29 ha) (Fig.1). OFR and FRG were once a single old-growth forest. However, large parts of the forest were clear-cut from the 1960s to 1980s and converted mainly into evergreen conifer plantations, which now surround the two forests (Fig. 1). OFR has been preserved as an old-growth temperate broad-leaved forest (Miyamoto and Sano, 2008), whereas FRG remains as strips of forest ranging from 5 to 200 m in width and 500 to 1500 m in length, primarily along the river and ridges. Such deforestation, followed by the establishment of evergreen conifer plantations, has been a very common human activity throughout Japan since the 1970s (Suzuki, 2002). FRG is connected to the main forest only by a very narrow corridor.

OFR and FRG are both deciduous broad-leaved forests. Species composition and structure in FRG are similar to those of OFR (Shibata et al., 2009). The dominant woody species in the canopy layer are *Quercus serrata*, *Fagus japonica*, *F. crenata*, *Q. crispula*, and *Castanea crenata*. Dwarf bamboos (*Sasa*, *Sasaella*, and *Sasamorpha* spp.) cover portions of the forest floor (Masaki et al., 1992). Disturbances related to human activity, such as logging, grazing, and fire, had been common around the forest until the 1930s (Suzuki, 2002). The species richness, abundance, and annual stability of forest birds in OFR are similar to those in primary or mature forests in low-montane areas of Honshu, suggesting that the original bird community is maintained in OFR (Tojo, 2009).

The surrounding plantations are pure stands of *Cryptomeria japonica* or *Chamaecyparis obtusa*. They are 20-40 years old, and their canopy has already been closed. In the surrounding secondary forests, the dominant woody species are *Q.serrata*, *Pinus densiflora* and *Carpinus laxiflora*. They are 5-60 years old.

2.2. Monitoring birds

To assess the abundance and species richness of birds, six and three bird census sites with similar topographic features were set in OFR and FRG, respectively (Fig.1). All the census sites were set as rectangles (40 m × 100 m), so that they could fit within the strip-shaped FRG. We conducted 15-minute point censuses in 3.5 h after sunrise at each site, from August to December 2006, June to

December 2007, and May to June 2008. We classified May to mid-August as the breeding season and late-August to December as the migratory season, by referring to the literatures (Kiyosu, 1966; Higuchi et al., 1997). For a single census, all birds found in the census site by either sight or call during the 15 minutes were identified to species level and recorded. We used the mean numbers of birds and species observed in 0.4 ha census in each forest as bird abundance and species richness. We categorized *Picoides leucotos*, *P. major* and *Picus awokera* as large woodpeckers in estimating the number of species, because we could not differentiate those species. The censuses were conducted 2 to 10 days per month and were intensified during the bird migratory season because the temporal variation in bird abundance was assumed to be greater. We attempted to balance the number of censuses between OFR and FRG: 9-11 and 18-21 per site at OFR and FRG, respectively, in the breeding season, and 25-31 and 52-56 per site at OFR and FRG in the migratory season. Consequently, 120 censuses were conducted in the breeding season (OFR: 60, FRG: 60) and 331 censuses were conducted in the migratory season (OFR: 167, FRG: 164).

We evaluated the relationship between forest shape effect and birds' migratory classes in the breeding and migratory season. We classified species by migration strategy into the following classes, using the information from Higuchi et al. (1997): (1) long-distance Palearctic or Paleotropical migrant; (2) short-distance temperate migrant; (3) non-migratory permanent resident. To compare the density and number of species of birds in each migratory class between OFR and

FRG in the two seasons, Wilcoxon signed-rank tests were performed. A Bonferroni adjustment among migratory class was employed in each comparison.

Secondly, to examine whether the bird body weight is associated with the habitat selection of each bird species in the two seasons, we calculated the OFR-FRG ratio: that is, the bird abundance of OFR divided by the bird abundance of OFR and FRG (e.g., if all birds in a focal species were observed only in OFR, this ratio would be 1, and if a focal species were observed at the same frequency in OFR and FRG, the ratio would be 0.5). We used the mean number of each species observed in OFR or FRG per site across the six/three sites (Appendix). In this analysis, species observed more than ten times in the season were included. The data of body weight came from Higuchi et al. (1997). We excluded *Garrulax canorus* from this analysis, because body weight information of this species was not available. We also excluded *Parus ater* are known to forage fruits of conifers and insects on their leaves (Higuchi et al. 1997), and thus prefer coniferous forests rather than broad-leaved forests (Yamaura et al., 2009). We did not observe other conifer-preferring bird species such as *Regulus regulus* and *Certhia familiaris* in the bird census. Spearman rank correlation was calculated between body weight and OFR-FRG ratio for migrants and residents separately. We did not distinguish between long-distance and short-distance migrants in this analysis because of their small sample sizes, and because of their relatively similar response to home range-related forest shape effect in terms of abundance and species richness (Table 1, Appendix). All statistical analyses were performed using R (R Development Core Team, 2008).

3. Results and Discussion

The abundance and number of species of birds in FRG were significantly lower than those in OFR in the breeding season (Table 1). This result suggests that irregular forest shape decreased the abundance and species richness of forest birds in the breeding season. If we assume that the birds return to the nest or cache to feed, a foraging area that is close to circular with the nest or cache at the center is optimal (Covich, 1976; Andersson, 1978). In an irregular-shaped forest, birds can not maintain their foraging area circular and thus they would not be able to forage with optimal efficiency (See Recher et al., 1987; Lindenmayer and Hobbs, 2004; Tubelis et al., 2007). Irregular forest shape may also discourage key social interactions such as mating (Recher et al., 1987). Due to the low resource utilization efficiency, birds may avoid FRG in the breeding season. On the other hand, differences in the abundance and number of species of birds between forests were not detected in the migratory season (Table 1). In the migratory season, birds need fewer resources because they just need to survive themselves than in the breeding season, when they nurture their chicks (see Gill, 2007), and thus the low resource utilization efficiency would not matter as much in the former. In addition, some bird species wintering in Japan are gregarious and wander to forage over a large area in a flock and are not territorial, i.e., they do not need to return to their nests or caches. These factors probably explain the similar bird abundance and species richness in OFR and FRG in the migratory season. We considered that the effect of the difference in forest area between OFR (ca. 98 ha) and FRG (ca. 29 ha) on bird abundance and species richness was minimal, if not negligible, because most of the forest birds in the study region are common in forests larger than 28 ha (See Yamaura et al. 2009).

In the breeding season, the abundance and number of species of long-distance and short-distance migrants in FRG were significantly lower than those in OFR, whereas no such tendency was observed for residents (Table 1). Among the residents, body weight and OFR-FRG ratio had a positive correlation (resident: $r_s = 0.84$, $S = 19.66$, $P < 0.01$, Fig. 2): Small residents preferred FRG or did not show forest preference. These results suggest that the response of forest birds to the shape of the forest might vary with bird traits. The residents may be able to utilize less represented foods because they know the habitat better (Tsujita et al. 2008). In addition, smaller residents, which have smaller foraging areas (see Schoener 1968; Holling, 1992), can maintain a close-to-circular foraging area even in very narrow forests. These factors may make them tolerant to the irregular shape of a forest. Among small residents, *P. montanus* clearly preferred FRG (Fig. 2, Appendix). *P. montanus* are known to eat wide variety of foods by their flexible foraging style (Higuchi et al., 1997). Therefore, *P. montanus* might use ample resources in irregular-shaped forests because their competitive migrants and large residents are absent there. In the migratory season, no forest shape effect was observed for any migratory class (Table 1). Body weight and OFR-FRG ratio of migrants and residents did not show a significant correlation (migrant: $r_s = -0.03$, $S = 123.01$, $P = 0.95$, resident: $r_s = 0.24$, $S = 124.88$, $P = 0.50$). Birds' lower resource needs and lower adhesion to their nests in the migratory season would make the forest shape effect less remarkable regardless of their traits.

Our study suggests that the irregular forest shape resulting from human activities negatively affect forest bird abundance and species richness even when the edge effect is weak, and that the effect varied with season and bird traits. It gives us caution that the effect of vegetation changes on the ecological roles of birds such as seed dispersal, pollination, and pest control (Sekercioglu, 2006) could also be different among seasons. At our study site, our previous study suggested that seed dispersal in the bird breeding season was depressed in FRG, whereas that in the migratory season was not (Naoe et al., 2011). Since the effects of conversion of natural forest to plantations seem to be less drastic than those of conversion to open pastures and agricultural fields, their impacts have tended to be underestimated. Careful consideration of various factors such as seasonality and bird traits is essential for evaluating the consequences of “mild” deforestation on birds and their ecological services.

Acknowledgments

We thank Ms. A. Sawa and Mr. H. Yamagata for field assistance; Drs. M. Ushio and R. Koda, E. Nakajima, Mr. T. F. Haraguchi, and members of the Center for Ecological Research for their valuable comments and discussion. We also thank the Ibaraki District Forestry Office for use of their facilities. Two anonymous reviewers and an editor provided constructive and helpful comments. Funding for this research was provided in part by the Ministry of Education, Culture, Sports, Science, and Technology Grant-in-Aid for Scientific Research (A-19201048, C-17570019), the Research Institute for Humanity and Nature (RIHN, P2-2), Global COE Program A06 of Kyoto University, and a JSPS Research Fellowship for Young Scientists to Shoji Naoe.

References

Andersson M (1978) Optimal foraging area: size and allocation of search effort. Theor Popul Biol 13: 397–409

Covich AP (1976) Analyzing Shapes of Foraging Areas: Some Ecological and Economic Theories. Annu Rev Ecol and Syst 7: 235–257

Gates JE, Gysel LW (1978) Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871–883

Gill FB (2007) Ornithology, 3rd edn. W.H. Freeman and Company, New York

Higuchi H, Morioka H, Yamagishi S (1997) The Encyclopaedia of Animals in Japan. Volume 4: Birds 2. Heibonsya limited, Tokyo

Holling CS (1992) Cross-scale morphology, geometry, and dynamics of ecosystems. Ecol Monogr 62: 447–502

Keller GS, Yahner RH (2007) Seasonal forest-patch use by birds in fragmented landscapes of south-central Pennsylvania. Wilson J Ornithol 119: 410–418

Keller GS, Ross BD, Klute DS, Yahner RH (2009) Temporal changes in migratory bird use of edges during spring and fall seasons in Pennsylvania. Northeast Nat 16: 535–552

Kiyosu Y (1966) Encyclopedia of wild birds. Tokyodo-shuppan, Tokyo

Lindenmayer DB, Cunningham RB, Donnelly CF, Nix H, Lindenmayer BD (2002) Effects of forest fragmentation on bird assemblages in a novel landscape context. Ecol Monogr 72: 1–18

Lindenmayer DB, Hobbs RJ (2004) Fauna conservation in Australian plantation forests – a review. Biol Conserv 119: 151–168

Masaki T, Suzuki W, Niiyama K, Iida S, Tanaka H, Nakashizuka T (1992) Community structure of a species-rich temperate forest, Ogawa Forest Reserve, central Japan. Vegetatio 98: 97–111

Miyamoto A, Sano M (2008) The influence of forest management on landscape structure in the cool–temperate forest region of central Japan. Landscape Urban Plan 86: 248–256

Moriguchi Y, Morishita T, Ohtani Y (2002) Climate in Ogawa Forest Reserve, In: Nakashizuka T, Matsumoto Y (eds) Diversity and interaction in a temperate forest community – Ogawa Forest Reserve of Japan –. Springer, Tokyo, pp 11–18

Murcia C (1995) Edge effects in fragmented forests: implications for conservation. Trends Ecol Evol 10: 58–62

Murgui E (2007) Effects of seasonality on the species-area relationship: a case study with birds in urban parks. Global Ecol Biogeogr 16: 319–329

Naoe S, Sakai S, Sawa A, Masaki T (2011) Seasonal difference in the effects of fragmentation on seed dispersal by birds in Japanese temperate forests. Ecol Res 26: 301–309

R Development Core Team (2008) R: a language and environment for statistical computing. R

Foundation for Statistical Computing, Vienna

Ranta P, Blom T, Niemelä J, Joensuu E, Siitonen M (1998) The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. Biodivers Conserv 7: 385–403

Recher HF, Shields J, Kavanagh RP, Webb G (1987) Retaining remnant mature forest for nature conservation at Eden, New South Wales: a review of theory and practice. In Saunders DA, Arnold GW, Burbidge AA, and Hopkins AJ (eds) Nature conservation: the role of remnants of vegetation. Surrey Beatty and Sons, Chipping Norton, pp 177–194

Ries L, Fletcher RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu Rev Ecol Evol Syst 35: 491–522

Schoener TW (1968) Sizes of feeding territories among birds. Ecology 49: 123–141

Sekercioglu CH (2006) Increasing awareness of avian ecological function. Trends Ecol Evol 21: 464–471

Shibata M, Kikuchi S, Tanaka H, Sueyoshi M, Yoshimaru H, Niiyama K (2009) Effects of population density, sex morph, and tree size on reproduction in a heterodichogamous maple, Acer mono, in a temperate forest of Japan. Ecol Res 24: 1–9

Suzuki W (2002) Forest vegetation in and around Ogawa Forest Reserve in relation to human impact, In: Nakashizuka T, Matsumoto Y (eds) Diversity and interaction in a temperate forest community – Ogawa Forest Reserve of Japan –. Springer, Tokyo, pp 27–41

Tojo H (2009) Breeding bird community of the Ogawa Forest Reserve, an old-growth deciduous forest in central Japan. Ornithol Sci 8: 105–115

Tsujita K, Sakai S, Kikuzawa K, 2008. Does individual variation in fruit profitability override color differences in avian choice of red or white *Ilex serrata* fruits? Ecol Res 23: 445–450

Tubelis DP, Lindenmayer DB, Cowling A (2007) The peninsula effect on bird species in native eucalypt forests in a wood production landscape in Australia. J Zool 271: 11–18

Yamaura Y, Ikeno S, Sano M, Okabe K, Ozaki K (2009) Bird responses to broad-leaved forest patch area in a plantation landscape across seasons. Biol Conserv 142: 2155–2165

Figure legends

Fig. 1 – Ogawa Forest Reserve (OFR) and surrounding landscape. The locations of the bird census sites in OFR and the fragmented forest (FRG) are indicated by dots.

Fig. 2 – Relationship between log body weight and OFR-FRG ratio in the breeding season. Note that each single point in the graphs means a bird species.

Fig. 1, Naoe et al.

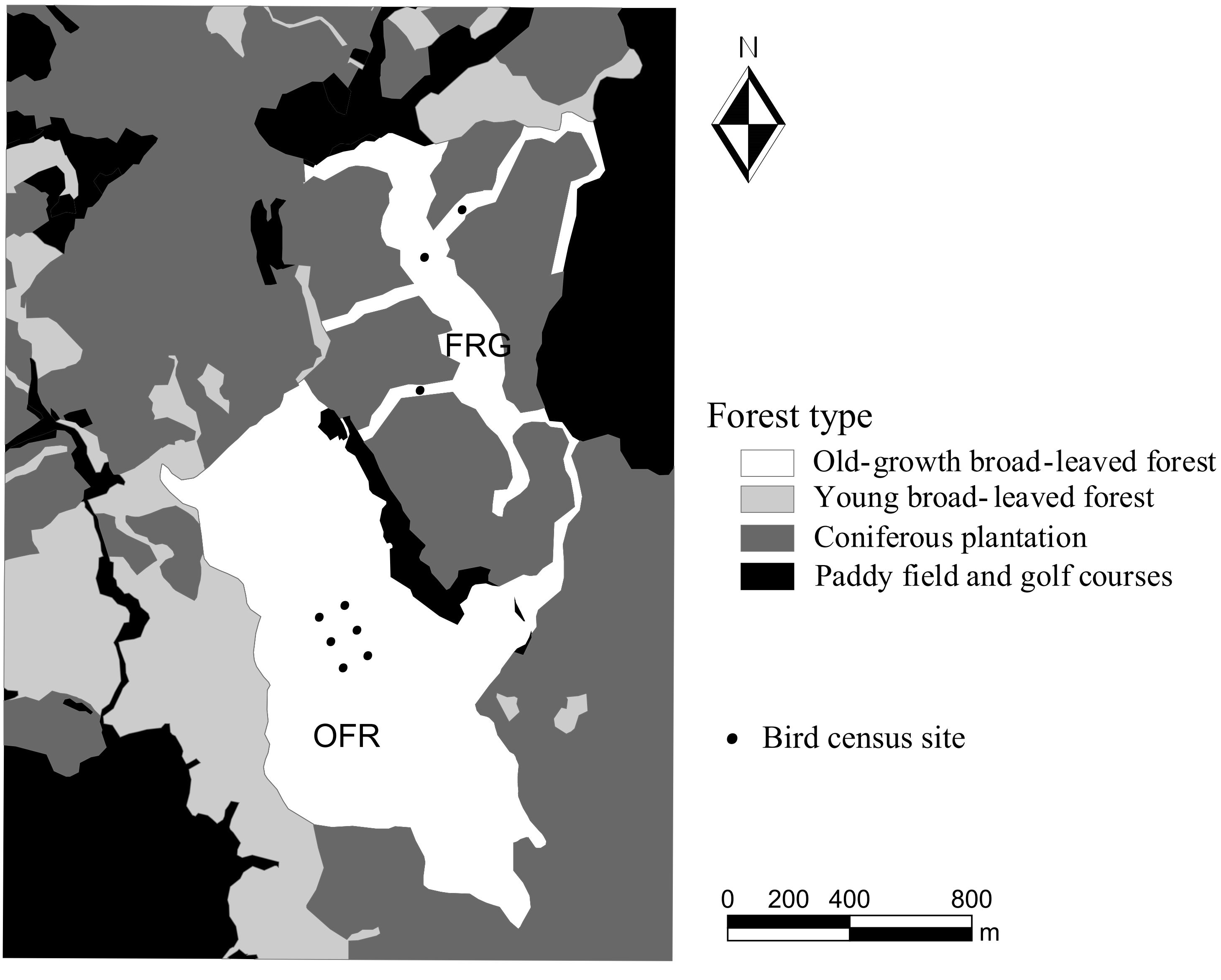

Fig. 2, Naoe et al.

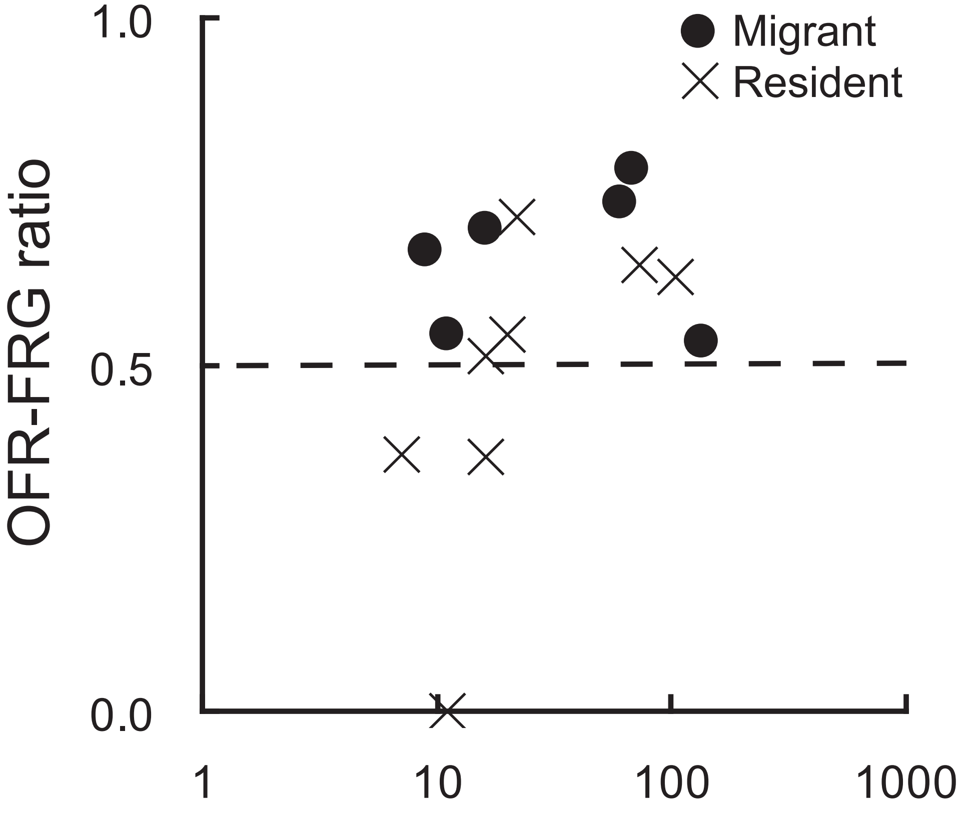

Table 1. Comparison between OFR and FRG in bird abundance and number of species in each migratory class in the breeding and migratory seasons.

	Breeding season				Migratory season			
Migratory class	Bird abundance (birds / 0.4 ha)		Number of species (species / 0.4 ha)		Bird abundance (birds / 0.4 ha)		Number of species (species / 0.4 ha)	
	OFR	FRG	OFR	FRG	OFR	FRG	OFR	FRG
Long-distance migrant	1.10 ± 0.14 *	0.60 ± 0.11	0.97 ± 0.11 *	0.58 ± 0.10	0.70 ± 0.17	0.45 ± 0.10	0.26 ± 0.05	0.19 ± 0.03
Short-distance migrant	1.13 ± 0.17 **	0.48 ± 0.10	0.75 ± 0.09 **	0.38 ± 0.08	1.05 ± 0.11	1.36 ± 0.13	0.67 ± 0.06	0.81 ± 0.07
Resident	2.27 ± 0.22	2.25 ± 0.25	1.65 ± 0.16	1.40 ± 0.15	2.69 ± 0.18	2.47 ± 0.22	1.63 ± 0.10	1.34 ± 0.11
Total	4.55 ± 0.34 *	3.40 ± 0.33	3.37 ± 0.23 **	2.37 ± 0.20	4.53 ± 0.31	4.35 ± 0.28	2.56 ± 0.15	2.34 ± 0.13

** $P < 0.01$; * $P < 0.05$.

In each comparison, we adjusted all *P* -values with the use of the Bonferroni test to control for type I error.

Appendix. Bird abundance (mean ± SE in OFR and FRG) and OFR-FRG ratio of each species in the breeding and migratory seasons, and body weight. Only species which we observed more than ten times in the breeding and/or migratory season are shown.

Migratory class	Species	Breeding season			Migratory season			Body Weight (g)
		Bird abundance (birds / 0.4 ha)		OFR-FRG ratio	Bird abundance (birds / 0.4 ha)		OFR-FRG ratio	
		OFR	FRG		OFR	FRG		
Long-distance migrant	*Turdus cardis*	0.27 ± 0.07	0.10 ± 0.03	0.73				60
	Ficedula narcissina	0.45 ± 0.10	0.20 ± 0.08	0.69				16
	Urosphena squameiceps	0.16 ± 0.06	0.08 ± 0.06	0.67				9
	Muscicapa dauurica				0.02 ± 0.01	0.05 ± 0.03	0.33	13
	Carduelis spinus				0.26 ± 0.11	0.07 ± 0.03	0.80	13
	Fringilla montifringilla				0.03 ± 0.03	0.06 ± 0.05	0.32	22
	Turdus naumanni				0.17 ± 0.04	0.11 ± 0.07	0.60	86
	Coccothraustes coccothraustes				0.09 ± 0.09	0.00 ± 0.00	1.00	55
Short-distance migrant	*Hypsipetes amaurotis*	0.83 ± 0.07	0.23 ± 0.11	0.78	0.31 ± 0.06	0.35 ± 0.04	0.47	68
	Zosterops japonica	0.20 ± 0.07	0.17 ± 0.06	0.54	0.42 ± 0.04	0.53 ± 0.09	0.44	11
	Garrulus glandarius	0.10 ± 0.04	0.09 ± 0.06	0.53	0.09 ± 0.04	0.33 ± 0.07	0.23	135
	Emberiza variabilis				0.13 ± 0.02	0.13 ± 0.02	0.50	29
Resident	*Parus major*	0.41 ± 0.06	0.39 ± 0.14	0.51	0.45 ± 0.07	0.37 ± 0.13	0.55	16
	Parus varius	0.18 ± 0.01	0.15 ± 0.08	0.54	0.17 ± 0.03	0.13 ± 0.01	0.57	20
	Parus montanus	0.00 ± 0.00	0.18 ± 0.09	0.00	0.12 ± 0.04	0.27 ± 0.05	0.31	11
	Parus ater	0.02 ± 0.02	0.15 ± 0.03	0.10				8
	Aegithalos caudatus	0.18 ± 0.06	0.31 ± 0.09	0.37	0.58 ± 0.08	0.45 ± 0.10	0.56	7
	Picoides leucotos, P. major, and Picus awokera	0.25 ± 0.05	0.15 ± 0.05	0.63	0.27 ± 0.06	0.19 ± 0.07	0.58	105
	Dendrocopos kizuki	0.50 ± 0.04	0.20 ± 0.03	0.71	0.38 ± 0.05	0.37 ± 0.16	0.51	22
	Eophona personata	0.28 ± 0.10	0.15 ± 0.08	0.64	0.20 ± 0.04	0.17 ± 0.07	0.53	73
	Cettia diphone	0.10 ± 0.04	0.18 ± 0.18	0.37	0.04 ± 0.01	0.05 ± 0.01	0.47	16
	Corvus macrorhynchos				0.06 ± 0.02	0.04 ± 0.03	0.59	675
	Streptopelia orientalis				0.01 ± 0.01	0.06 ± 0.02	0.18	225
	Garrulax canorus				0.03 ± 0.03	0.06 ± 0.01	0.37	unknown