ORIGINAL ARTICLE

The effects of a typhoon (9918 Bart, 1999) on the bird community in a warm temperate forest, Southern Japan

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ORNITHOLOGICAL SCIENCE

Abstract The effects of a severe typhoon (9918 Bart) on a bird community in a warm temperate forest, southern Japan, in 1999, were investigated. The total abundance and number of species showed clear seasonality in normal years, and were higher during winter mostly due to the influx of winter visitor species. The composition of dietary and foraging guilds also changed among seasons. Among the dietary guilds, frugivores/granivores and omnivores increased in winter, whereas insectivores decreased in winter. As for the foraging guilds, forest interior- or edge-dependent species increased in winter, whereas generalists remained constant. Therefore, I examined the effects of typhoon 9918 Bart in winter and in summer, comparing the data sets from three years before and two years after its passage. In the first winter after the typhoon, the abundance of birds was significantly lower than in all three control years, however it recovered to the same level as the control years in the second winter. In contrast, in both the first and second summer after the typhoon, bird abundance was significantly higher than in the control years. The effects of the typhoon also differed among the dietary and foraging guilds. The winter dominant frugivores/granivores were fewer in the first winter leading to a decrease in total bird abundance in that season, whereas the increase in omnivores and insectivores resulted in the increased total bird abundance in summer. The reduction in forest interior-dependent species led to the lower total abundance in winter, and the increase in forest edge-dependent species may have led to the increase in total bird abundance both in winter and in summer. These different responses among different foraging and dietary guilds affected total bird abundance in concert. The disturbance event (typhoon) appeared to cause opposing effects on total bird abundance in winter and in summer.

Key words Bird community, Dietary and foraging guilds, Seasonal change, Typhoon disturbance, Warm temperate forest

Natural disturbance is known to be an important agent leading to habitat heterogeneity in forest ecosystems (Greenberg & Lanham 2001), and has a profound impact on the abundance and distribution of individuals (Jones et al. 2001). The severe disturbance in the form of storms (ie winds of, or exceeding 25 m/s, often accompanied by heavy rain) is, therefore, among the most influential factors in determining the structure and species composition of forest biotic communities (White 1979; Tanner et al. 1991). Bird populations are also affected by storms, although species may differ in their response to the disturbance depending on the severity of the storm and the ecological niche of each species (Tejeda-Cruz & Sutherland 2005). The effects of storms often differ among dietary guilds: frugivores, nectarivores, and granivores are more vulnerable than insectivores and omnivores, since strong storm-force winds strip flowers, fruits, and seeds from plants which leads to an immediate food shortage for those species (Askins & Ewert 1991; Lynch 1991; Waide 1991; Wunderle et al. 1992; Wunderle 1995; Tejeda-Cruz & Sutherland 2005). Insectivorous and omnivorous species appear to be more resilient to disturbance, because their food resources are more diverse and have high turnover rates in storm disturbed areas and in tree-fall gaps (Thompson 1983; Waide 1991; Wunderle et al. 1992; Greenberg & Lanham 2001). Storms of 25 m/s or more may also blow off large quantities of leaves

(Received 25 March 2005; Accepted 28 July 2005)

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and branches, may break limbs and main stems, and, if sufficiently strong, even blow down trees. These events can lead to changes in micro-habitat distributions in forests, and influence the fate of each foraging and breeding guild thereafter. The forest interior-dependent species, especially the understory species, often decrease, whereas forest edge-dependent or early successional species increase after disturbance by a storm (Canterbury & Blockstein 1997; Greenberg & Lanham 2001; Faccio 2003; Tejeda-Cruz & Sutherland 2005). The drastic loss of foliage from the canopy forces canopy foragers to shift their foraging habitat to the forest understory (Waide 1991; Wunderle 1995). As a result of increased habitat heterogeneity and higher levels of productivity around tree fall gaps (Blake & Hoppes 1986; Greenberg &Lanham 2001), species richness, species diversity, and even total abundance in some cases, tends to increase after disturbance by storms (Wunderle 1995; Greenberg & Lanham 2001; Faccio 2003).

Most previous studies have focused on a single specific season, such as the summer breeding season (e.g. Canterbury & Blockstein 1997; Faccio 2003; Tejeda-Cruz & Sutherland 2005), the spring or fall migration seasons (e.g. Blake & Hoppes 1986) or the winter (e.g. Askins & Ewert 1991; Lynch 1991; Wunderle et al. 1992), presumably due to the availability of baseline data. Waide (1991) and Wunderle (1995) followed the post-disturbance changes to a bird community for more than a year, but they did not identify the different impacts of storm effect in different seasons. Regional bird communities often exhibit drastic changes between seasons resulting from the movement of migrants (e.g. Thompson & Willson 1979; Newton & Dale 1996a, b). The same extent of storm disturbance may affect bird communities differently in different seasons. In order to examine the effects of storm disturbance on a forest bird community, therefore, the seasonal differences of its effects should be taken into consideration

The passage of a severe typhoon (9918 Bart) through Kyushu, the southernmost of the four main Japanese islands, in September 1999, provided a rare opportunity to reveal the effects of a typhoon on a bird community in a seasonally distinctive environment, since I had already collected baseline census data during the three years prior to its passage. The aims of the present paper are: 1) to describe the seasonal trends of the bird community in a warm temperate forest before the typhoon's passage, based on monthly censuses, 2) to identify the common species as belonging to particular dietary and foraging guilds based on the literature and on observations made prior to the typhoon, 3) to compare the effects of the typhoon disturbance between different seasons, examining the results of a five-year annual census, three years before and two years after its passage, and 4) to discuss the influence of foraging and dietary guild composition in each season on seasonal differences in post-typhoon changes in bird abundance.

METHODS

1) Study site

The study was carried out in Tatsutayama Experimental Forest in Kumamoto City, Kyushu, Japan (Fig.1, 32°49′N, 130°44′N, 28.4 ha, 48–152 m asl). Tatsutayama is an isolated hill forest area of about 450 ha, and the Experimental Forest is located on the southwestern slope of this hill. The hill is mostly covered with secondary evergreen broad-leaved forests, 40–50 years of age, with some small patches of coniferous and deciduous plantations. The dominant canopy tree species is *Castanopsis cuspidata*, with an average height of 17 m (Seki & Sato 2002), while *Quercus glauca* and *Ilex chinensis* are common sub-canopy species. Young individuals of canopy and sub-canopy tree species also dominated in the forest understory, followed by two fruiting shrubs (*Eurya japonica* and *Symplocos lucida*). At the forest edge, and in some patches of deciduous trees such as *Quer-*

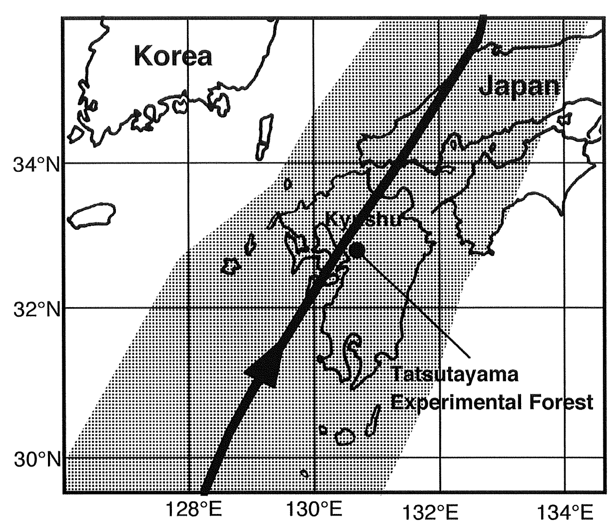

Fig. 1. Path of Typhoon 9918 Bart over Kyushu, September 1999. The solid line indicates the approximate course of the typhoon eye, and the shaded area shows the movement of the storm zone with an average wind speed of over 25 m/s.

cus serrata, the forest understory was densely covered with *Pleioblastus* spp. and shrubs (personal observation).

On 24 September 1999, a severe typhoon (9918 Bart) struck Kyushu, and its eye passed less than 40 km to the north of the Tatsutayama Experimental Forest (Fig. 1). During its passage, the lowest air pressure recorded in Kyushu was 944 h Pa and the maximum wind speed was 66.2 m/s, while the lowest pressure in Kumamoto City was 956 h Pa, and the greatest wind speed was 49.0 m/s (Japan Meteorological Agency 1999). Typhoons of such severity are very rare in Kumamoto City; the return period of typhoons with a maximum wind speed of over 50.0 m/s is considered to be more than 100 years (Saito & Kominami 2004). As a consequence of the 24 September 1999 typhoon, at the study site 13.6% of the canopy trees died and 72.7% were severely damaged. Most of the surviving trees were extensively defoliated by the typhoon's strong winds, and the annual litter fall in 1999 was 1.3- to 2.0 times greater than in normal years (Seki & Sato 2002). As a result of this destruction, average canopy cover was greatly reduced. Whereas more than 60% of the forest trails used during bird censuses were covered with closed canopy in 1997, this proportion was reduced to just 14% in 2001. In addition to the modification of canopy cover, the understory vegetation was also changed; in 1997, 74% of the trail sides consisted of open understory with sparsely distributed shrubs, whereas this percentage had fallen to 52% in 2001, and dense dwarf bamboo *Sasa* spp. and scrub vegetation had increased instead (personal observation).

2) Seasonal bird censuses

Bird censuses were made 2–4 times each month, from November 1996 to June 1998, along a 3.8 km course, in order to study the seasonal changes in the area's bird community. The species and number of birds seen or heard within 25 m of either side of the census route were recorded while walking slowly at an average speed of 2.0 km/hr. Censuses were begun at sunrise for most of the research period, although the starting time was delayed for 1 h during the winter (November to February), because bird activity was very low at sunrise during the coldest part of the winter. In this study area the undergrowth was not dense, therefore I assumed that the detectability of birds within 25 m of the transect line was high and constant, and that the number of birds recorded within the area reflected their relative density.

3) Annual bird censuses

Annual bird censuses were used to examine the changes in the bird community among years, and also to determine the effects of the typhoon. Two distinct periods were chosen for annual censuses, based on the seasonal bird surveys: 1) the summer period between 16 May and 30 June, when breeding activity was most conspicuous, and 2) the winter period between 16 November and 31 December, when wintering bird populations reached their peak. The same route was surveyed (using the same methods as described above) six times in each summer and winter period from 1996 to 2001, with the exception of summer 1998, when only five censuses were conducted because of bad weather. Since I could not find any appropriate control sites against which to evaluate the effects of the typhoon, I compared the data sets from the five years, defining the initial three years as control years and the remaining two years as disturbed years.

4) Foraging and dietary guilds

Since the influence of habitat changes resulting from storm disturbance often differs among dietary and foraging guilds (Askins & Ewert 1991; Tejeda-Cruz & Sutherland 2005), I categorized the common bird species occurring in the study area with an abundance of more than 20 individuals/km^2 on average in every control year, into three groups based on dietary guilds and also into three groups based on foraging guilds, in winter and in summer separately. Dietary guilds were defined following Nakamura and Nakamura (1995) and Kiyosu (1966); species which largely feed on fruits and seeds were defined as frugivores/granivores, those sometimes eating plant foods were considered to be omnivores, those seldom eating plant foods were insectivores.

I compared each species' dependence on the forest interior or the forest edge habitat as foraging sites, using the data from three control years, and identified the foraging guild for each season. The census route was established along a forest management trail, with various widths of canopy opening: 61.6% of the route consisted of narrow trail with closed canopy before the typhoon, 18.7% consisted of wide vehicle trails but with less than 5 m of canopy opening along the trail, 19.7% consisted of wide trail with 5–15 m of disturbed trail edge areas. I picked up two subsets of census records, one from the closed canopy section of the census route as forest interior habitat, 490 m long, and another from the section with 5–15 m of disturbed trail edge as forest edge habitat, 560 m long. I, then, compared the abundance in the two habitats for each species, and defined three foraging guilds as follows: a) forest interior-dependent species that were significantly more abundant in the forest interior, b) forest edge-dependent species that were significantly more abundant along the forest edge, and c) generalist species that were not significantly different in abundance between the two habitats.

5) Statistics

The Kruskal–Wallis test was used to analyze annual variation in total abundance, number of species, and abundance of each species or guild within control years. Priori comparisons were made to examine the effects of the 1999 typhoon on bird populations, using the Mann–Whitney U test. To reduce the possibility of misidentifying the annual variation as an effect of the typhoon, I regarded only those species, for which the density in either disturbed year was significantly different from that of all three control years, as having been affected by the typhoon. This procedure would also be effective in reducing the possibility of type I error, caused by making a large number of statistical comparisons. The Wilcoxon signed rank test was used to compare bird abundance in the forest interior and at the forest edge. Only the abundance of common species was analyzed separately; uncommon species were excluded from individual analysis and were listed in Appendix 1.

RESULTS

1) Seasonality and variation in the bird community during control years

From November 1996 to June 1998, the abundance of birds and the number of species showed clear seasonality (Fig. 2). Total bird density was low (about 700–1000 birds per km^2), from April to September, increased in autumn and was highest (about 1500–2500 birds per km^2) from November to January. Based on the categorization of the status of each species at the study site (Appendix 1), the increased density during winter was mostly due to the increase in the number of winter visitors.

In the winters of the three control years, 1811–2072 birds per km^2, and 22.7–25.8 species per census were recorded on average in each year. The total abundance of birds differed significantly even among control years, but the number of species was independent of year (Fig. 3). The 17 species shown in Fig. 3 were common in winter and were analyzed separately. Both the Brown-eared Bulbul *Hypsipetes amaurotis* and the Japanese White-eye *Zosterops*

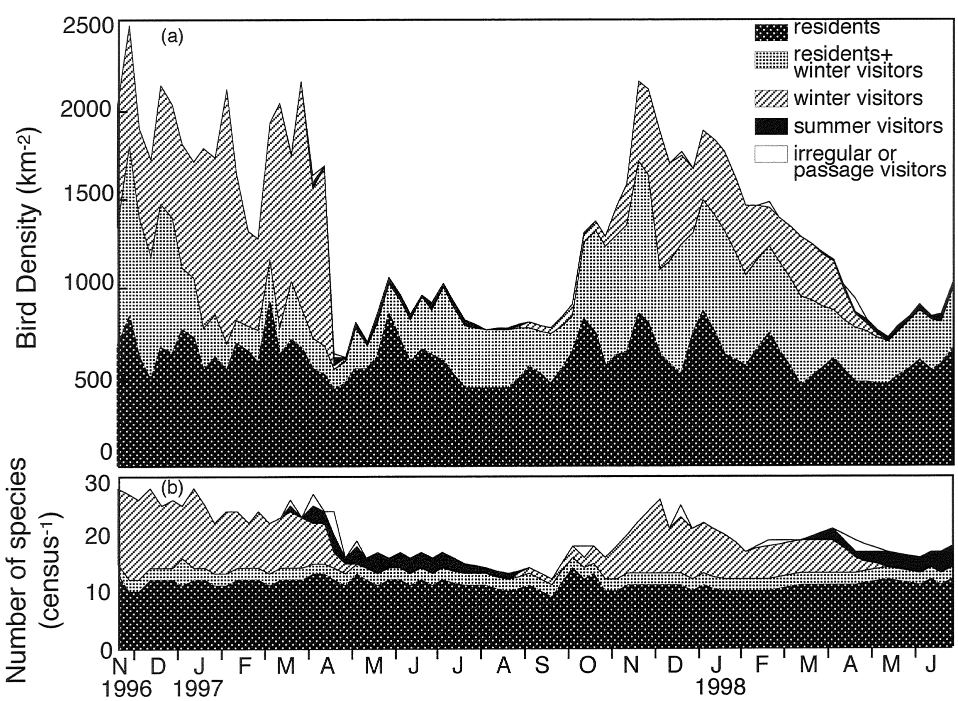

Fig. 2. Seasonal variation in: (a) the number of individuals per km^2, and (b) the number of species per census, observed along the census route, in three control years.

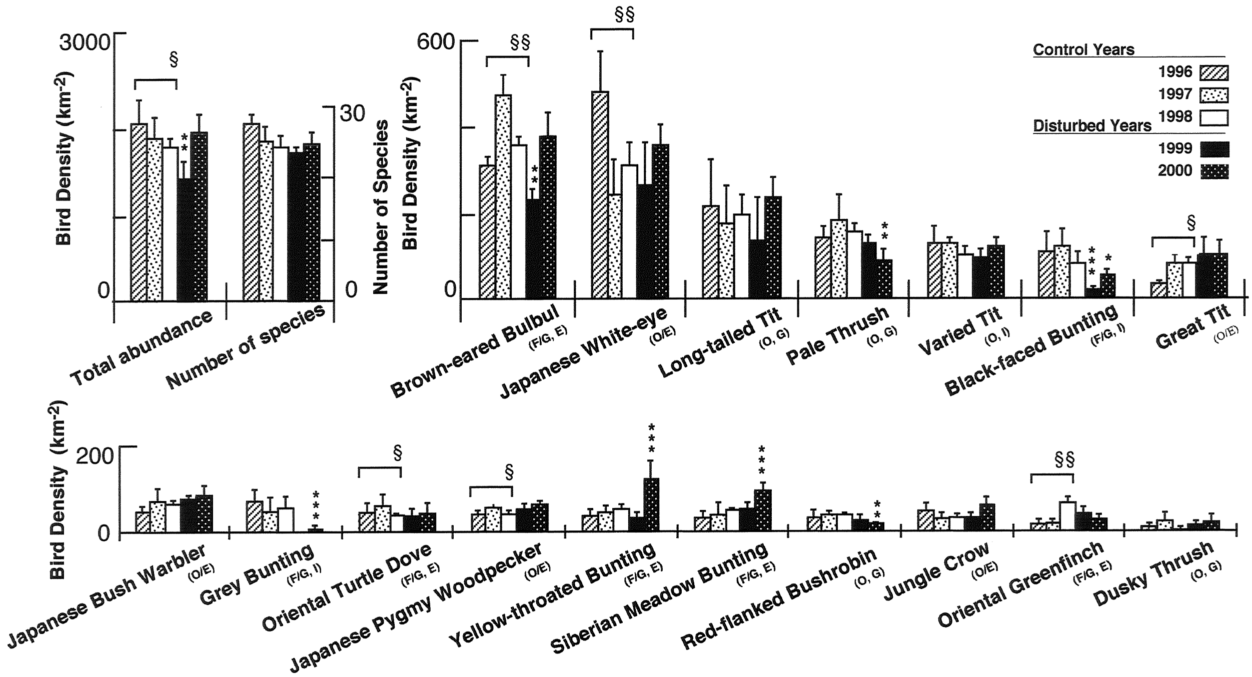

Fig. 3. Differences in bird density, and in number of species observed, in winter, between control years and the disturbed year. Section signs show significant differences among control years by Kruskal–Wallis test; §: P<0.05 and §§: P<0.01. Asterisks indicate significant differences or tendencies towards difference between the disturbed year and all three control years by Mann–Whitney U test; *: P<0.1, **: P<0.05 and ***: P<0.01. Letters in parenthesis under a species' name indicate the dietary and foraging guilds of each species based on Table 1: frugivore/granivore (F/G), omnivore (O), and insectivore (Is), and forest interior-dependent species (I), generalist species (G), and forest edge-dependent species (E).

japonicus have resident populations supplemented by wintering populations of the same species; their abundance differed greatly from year to year, which was one of the major causes of total abundance variation. Four out of nine common residents, the Great Tit *Parus major*, Oriental Turtle Dove *Streptopelia orientalis*, Japanese Pygmy Woodpecker *Dendrocopos kizuki*, and Oriental Greenfinch *Carduelis sinica*, also differed significantly in their abundance with the year, but their ranges were small compared to those of the bulbul and white-eye. The winter visitor species were relatively stable in abundance, and the difference between years was significant for only one (Dusky Thrush *Turdus naumanni*) out of six common wintering species.

In the three control year summers, 877–930 birds per km^2, and 16.5–17.0 species per census were recorded on average in each year. Neither bird abundance nor the number of species observed differed with the year (Fig. 4). The 13 resident species shown in Fig. 4 were common during summer, and three of them (Eurasian Tree Sparrow *Passer montanus*, Oriental Greenfinch, and Chinese Bamboo Partridge *Bambusicola thoracica*) differed significantly in abundance between years.

2) The dietary and foraging guilds in each season

Among the 17 common species in winter, seven were defined as frugivore/granivore and 10 as omnivores; none was defined as an insectivore because all fed on at least some fruits and seeds in winter (Table 1). Among the 13 common species in summer, only two were defined as frugivore/granivore, four were omnivores, and seven were insectivores (Table 2). The abundance of frugivores/granivores and omnivores increased in winter, whereas insectivores increased in summer.

The common species in each season were also grouped into three foraging guilds. Among the 17 common species in winter, the Grey Bunting *Emberiza variabilis*, Varied Tit *Parus varius*, and Black-faced Bunting *Emberiza spodocephala* were significantly abundant in the forest interior habitat, and were classified as forest interior-dependent species

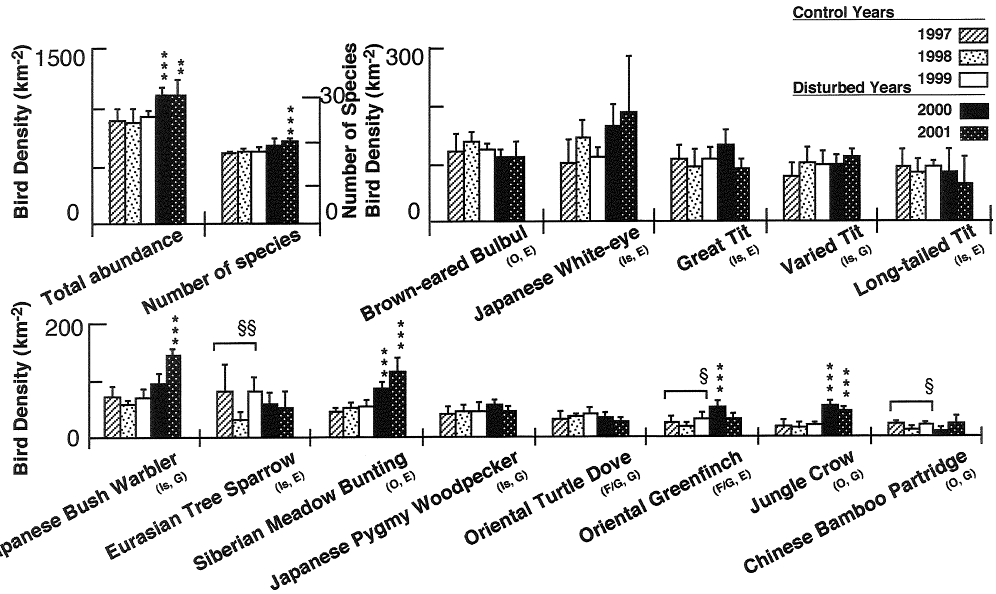

Fig. 4. Differences in bird density, and in number of species observed, in summer, between control years and the disturbed year. Section signs show significant differences among control years by Kruskal–Wallis test; §: P<0.05 and §§: P<0.01. Asterisks indicate significant differences between the disturbed year and all three control years by Mann–Whitney U test; *: P<0.05 and **: P<0.01. Letters in parenthesis under a species' name indicate the dietary and foraging guilds of each species based on Table 2: frugivore/granivore (F/G), omnivore (O), and insectivore (Is), and forest interior-dependent species (I), generalist species (G), and forest edge-dependent species (E).

Table 1. The foraging and dietary guilds identification of each common species in winter. The foraging guild of each species was categorized into each of three groups, following the results of bird density comparison between forest edge and forest interior habitat, using Wilcoxon signed rank test: forest interior-dependent species (I), generalist species (G), forest edge-dependent species (E). The dietary guild of each species was also identified from the following three groups based on the literatures: frugivore/granivore (F/G), omonivore (O), and insectivore (Is).

Species	Mean density (km^{-2})		P	Foraging guild	Dietary guild
	Edge	Interior			
Grey Bunting	18	179	<0.001	I	F/G
Varied Tit	71	215	0.001	I	O
Black-faced Bunting	103	195	0.05	I	F/G
Red-flanked Bushrobin	36	61	>0.1	G	O
Dusky Thrush	16	25	>0.1	G	O
Long-tailed Tit	278	413	>0.1	G	O
Pale Thrush	187	209	>0.1	G	O
Yellow-throated Bunting	75	43	0.05	E	F/G
Japanese Bush Warbler	93	73	0.02	E	O
Japanese Pygmy Woodpecker	81	48	0.01	E	O
Great Tit	143	77	0.005	E	O
Jungle Crow	97	57	0.004	E	O
Japanese White-eye	645	331	<0.001	E	O
Brown-eared Bulbul	736	327	<0.001	E	F/G
Oriental Turtle Dove	137	14	<0.001	E	F/G
Oriental Greenfinch	145	9	<0.001	E	F/G
Siberian Meadow Bunting	67	2	<0.001	E	F/G

Table 2. Their foraging and dietary guilds identification of each common species in summer. The foraging guild of each species was categorized into each of three groups, following the results of bird density comparison between forest edge and forest interior habitat, using Wilcoxon signed rank test: forest interior-dependent species (I), generalist species (G), forest edge-dependent species (E). The dietary guild of each species was also identified from the following three groups based on the literature: frugivore/granivore (F/G), omonivore (O), and insectivore (Is).

Species	Mean density (km^{-2})		P	Foraging guild	Dietary guild
	Edge	Interior			
Chinese Bamboo Partridge	29	31	>0.1	G	O
Jungle Crow	42	38	>0.1	G	O
Japanese Bush Warbler	105	86	>0.1	G	Is
Long-tailed Tit	239	137	>0.1	G	Is
Japanese Pygmy Woodpecker	92	46	>0.1	G	Is
Oriental Turtle Dove	92	59	>0.1	G	F/G
Great Tit	181	120	0.04	E	Is
Oriental Greenfinch	80	43	0.04	E	F/G
Japanese White-eye	185	137	0.02	E	Is
Varied Tit	208	72	0.005	E	Is
Brown-eared Bulbul	330	130	0.001	E	O
Siberian Meadow Bunting	116	14	0.001	E	O
Eurasian Tree Sparrow	118	10	0.001	E	Is

(Table 1). Four other species, the Red-flanked Bushrobin *Tarsiger cyanurus*, Dusky Thrush, Long-tailed Tit *Aegithalos caudatus*, and Pale Thrush *Turdus pallidus*, were often observed in both the forest interior and forest edge; their abundance did not differ significantly between the habitats, and, therefore, they were classified as generalist species. The ten remaining species were significantly abundant at the forest edge, and were classified as forest edge-dependent species.

None of the common species in summer was significantly abundant in the forest interior (Table 2). The abundance of six species, the Chinese Bamboo Partridge, Jungle Crow *Corvus macrorhynchos*, Japanese Bush Warbler *Cettia diphone*, Long-tailed Tit, Japanese Pygmy Woodpecker, and Oriental Turtle Dove did not differ significantly between the habitats, and they were classified as generalist species. The seven remaining species were significantly abundant in the forest edge, and were classified as forest edge-dependent species. Among these foraging guilds, forest interior- or edge-dependent species increased in abundance during winter, whereas the abundance of generalist remained constant.

3) The effects of typhoon 9918 Bart on the bird community in winter

In the winter of 1999, 2–3 months after the passage of typhoon 9918 Bart, the population of birds and the number of species recorded was the lowest among the five years, averaging 1427 birds per km^2 and 21.5 species per census. The total abundance of birds was significantly lower than in all of the control years, but the number of species was not (Fig. 3). Among the 17 common species, Black-faced Bunting and Brown-eared Bulbul, were significantly less abundant in 1999 than in every control year, and the Grey Bunting was not observed at all in 1999. None of the common species was significantly more abundant in 1999 than in the control years.

In the winter of 2000, 14–15 months after the typhoon, the total abundance of birds and the number of species had recovered to 1961 birds per km^2 and 22.8 species per census. Neither the abundance nor the number of species observed differed significantly from the controls years (Fig. 3). The composition of the bird community, however, was not the same as during the control years: four species, the Grey Bunting, Black-faced Bunting, Pale Thrush, and Red-flanked Bushrobin were significantly less abundant in 2000 than in each of the control years (Fig. 3), whereas the Siberian Meadow Bunting *Emberiza cioides* and Yellow-throated Bunting *Emberiza elegans* were both significantly more abundant than in all of the control years.

4) The effects of typhoon 9918 Bart on the bird community in summer

In the summer of 2000, 8–9 months after the typhoon, both the abundance (1112 birds per km^2) and the number of species (18.3 species per census on average) were higher than in the control years. The differences in bird abundance between 2000 and every control year were significant, but the differences between the numbers of species were not (Fig. 4). Three species among the 13 common species, the Jungle Crow, Siberian Meadow Bunting, and Oriental Greenfinch, were significantly more abundant in summer 2000 than in the control years. None of the common species showed a significant decrease in 2000.

In the summer of 2001, 20–21 months after typhoon 9918 Bart, both the abundance (1124 birds per km^2) and the number of species (19.2 species per census on average), were still high, showing a significant difference from those in any of the control years (Fig. 4). Three of the common species, the Jungle Crow, Siberian Meadow Bunting, and Japanese Bush Warbler, were significantly more abundant than in any of the control years. Again, none of the common species had decreased significantly in abundance when compared with the control years.

5) The difference of typhoon effects among dietary and foraging guilds

The abundance of frugivores/granivores in the winter of 1999, following typhoon 9918 Bart, was significantly lower than in all of the control years (Fig. 5a), although the abundance of this group also differed significantly even among control years. In the winter of 2000, the abundance of frugivores/granivores recovered to pre-typhoon winter levels, and did not differ significantly from any of the control years. In the summers of 2000 and 2001, the total abundance of omnivores was significantly higher than in the three control years (Fig. 5b).

In the winter of 1999, the total abundance of forest interior-dependent species was significantly lower than in the control years, and generalist and forest edge-dependent species were also at their lowest recorded levels (see Fig. 6). The significant decrease in forest interior-dependent species in winter was also observed in 2000. In the winter of 2000, the forest edge-dependent species tended to increase, although their abundance did not differ significantly from that of 1997 ($P<0.07$). In the summer of 2000, the total abundance of forest edge-dependent species was significantly higher. In the next summer, 2001, the abundance of forest edge-dependent species was high, although it did not differ significantly from one of the control years, 1998 ($P=0.11$).

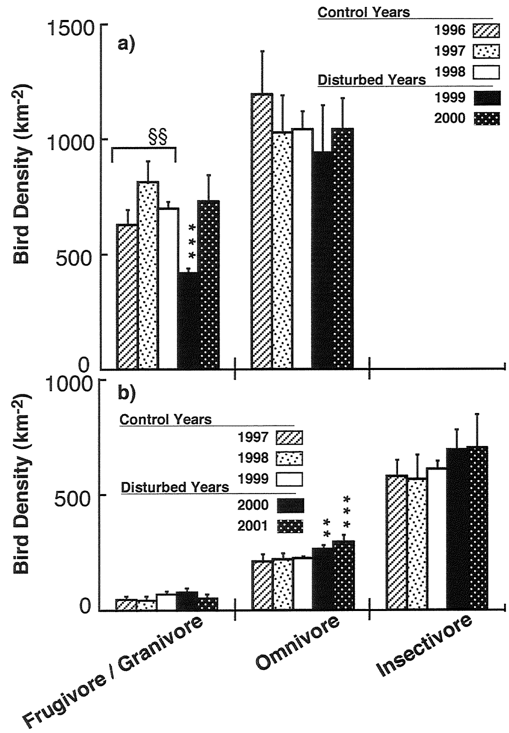

Fig. 5. The difference in bird density of each dietary guild between the control years and the disturbed year: a) in winter and b) in summer. Section signs indicate significant differences among control years by Kruskal–Wallis test; §: $P<0.05$ and §§: $P<0.01$. Asterisks indicate significant differences between the disturbed year and all three control years by Mann–Whitney U test; *: $P<0.05$ and **: $P<0.01$. Letters in parenthesis under a species' name indicate the dietary and foraging guilds of each species based on Table 2: frugivore/granivore (F/G), omnivore (O), and insectivore (Is), and forest interior-dependent species (I), generalist species (G), and forest edge-dependent species (E).

DISCUSSION

The bird community at the study site in Kyushu, Japan, showed clear seasonality in normal years, because the total abundance and the number of species increased during winter due to the influx of winter visitors. This was similar to results from other warm temperate forests in Yakushima, Japan, and Hong Kong, China (Noma & Yumoto 1997; Kwok & Corlett 1999). This change in total abundance was accompanied by a modification of the dietary and foraging guild composition. Frugivores/granivores and

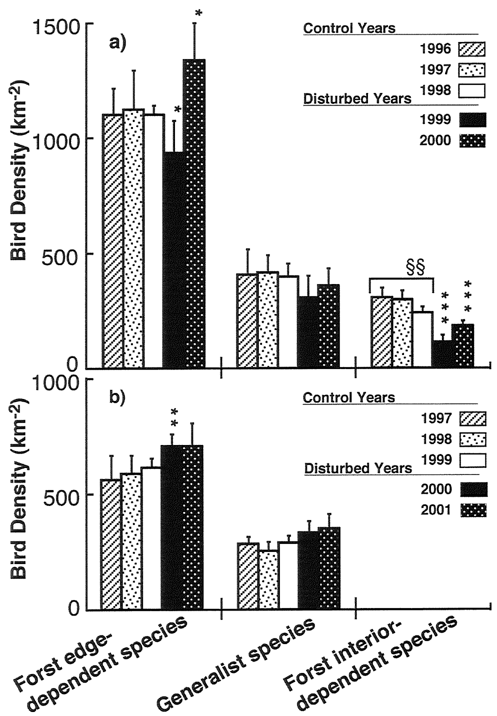

Fig. 6. The difference in bird density of each foraging guild between the control years and the disturbed year: a) in winter and b) in summer. Section signs indicate significant differences among control years by Kruskal–Wallis test; §: $P<0.05$ and §§: $P<0.01$. Asterisks indicate significant differences between the disturbed year and all three control years by Mann–Whitney U test; *: $P<0.05$ and **: $P<0.01$. Letters in parenthesis under a species' name indicate the dietary and foraging guilds of each species based on Table 2: frugivore/granivore (F/G), omnivore (O), and insectivore (Is), and forest interior-dependent species (I), generalist species (G), and forest edge-dependent species (E).

omnivores increased in winter, whereas insectivores increased in summer, both in their abundance and the number of species (Table 1; Fig. 5). Both fruit and nut production is known to increase from autumn to winter in warm temperate forests (Noma & Yumoto 1997; Kominami et al. 2003), and the increase in frugivores/granivores and omnivores in winter coincided with the ripening period of these plant foods. The observed increase of omnivores in winter might have been affected by a dietary shift to plant foods, as many passerine birds are mostly insectivorous during the summer chick rearing period (Tables 1 & 2). As for the foraging guilds, forest interior- or edge-dependent species increased in abundance during winter, whereas the abundance of generalists remained constant (Table 2; Fig. 6). These changes in foraging guilds also appear to have been affected by the movement of wintering species; the increase in forest interior species in winter may have largely been affected by the presence of two buntings, Grey Bunting and Black-faced Bunting, while the increase in edge-dependent species in winter appears to have been due to the attendance of large flocks of Brown-eared Bulbul and Japanese White-eye.

The effects of typhoon 9918 Bart also differed largely between seasons. The total abundance of birds decreased in the first winter after the typhoon's passage and then recovered to levels equivalent to those prior to disturbance by the second winter (Fig. 3), whereas total bird abundance increased both in the first and second summer after the typhoon (Fig. 4). The typhoon's effects on forest habitat would have been the same both in winter and in summer, and, therefore, these different trends in bird abundance between the two seasons may have resulted from seasonal changes in the dietary and foraging guilds' compositions acting through differences in post-typhoon responses among these guilds.

Among the three dietary guilds examined, the abundance of winter frugivores/granivores was reduced shortly after the typhoon, in the winter of 1999, but recovered in the following winter. The decrease in the total abundance of birds in winter 1999 appears to have been due to a decrease among the winter dominant frugivore/granivore species, and the recovery of total abundance in the second winter coincided with the recovery of frugivores/granivores. Previous studies have also reported a decrease in frugivores and granivores shortly after a storm and their quick recovery, along with the decrease and recovery of plant food (Levey 1988; Askins & Ewert 1991; Lynch 1991; Waide 1991; Wunderle et al. 1992; Wunderle 1995; Tejeda-Cruz & Sutherland 2005). The observed post-typhoon change in frugivore/granivore abundance in the present study may also have been due to changes in plant food abundance, although I did not examine food abundance. During the summer, omnivores and insectivores were recorded at maximal levels after typhoon 9918 Bart, and omnivores also significantly increased. The increase in total abundance in the first and second summers after the typhoon can be explained partly by the tendency among omnivores and insectivores to increase and predominate in summer, which may be related to expected increases in arthropod productivity commonly observed in storm-disturbed areas during summer season (Levey 1988; Greenberg & Lanham 2001).

Some results, however, cannot be explained by difference in responses among dietary guilds. In the frugivore/granivore guild in winter, the Brown-eared Bulbul, which strongly depends on fruits and nectar in the canopy, is the only species that followed the overall pattern of initial decreased followed by recovery. Both the Grey, and Black-faced buntings were significantly reduced or tended to decrease ($P<0.01$ and $P<0.09$ respectively) even in the second winter after the typhoon. In contrast, neither the Yellow-throated, nor the Siberian Meadow bunting showed significant change in abundance even in the first winter and then increased in the second winter after the typhoon. The hypothesized increase in arthropod abundance during summer is unlikely to be the only factor influencing the increase in insectivores and omnivores, because insectivores showed only a marginal change in abundance whereas omnivores increased significantly. These results may be explained largely by the interplay of the diets and foraging niches of each species.

Among the three foraging guilds, forest edge-dependent species significantly or marginally increased in most of the seasons studied, except in winter 1999 shortly after the disturbance. The forest-interior species, by contrast, significantly decreased during the first and second winter after typhoon 9918 Bart. Such increases in forest edge-dependent species and decreases in forest-interior dependent species, are commonly observed in storm disturbed forests, along with a drastic loss and slow recovery of the canopy foliage and a rapid increase of understory vegetation (Canterbury & Blockstein 1997; Greenberg & Lanham 2001; Faccio 2003; Tejeda-Cruz & Sutherland 2005). The observed difference in post-typhoon responses among frugivore/granivore species may have been related to this difference among foraging guild; the forest interior-dependent species, Grey Bunting and Black-faced Bunting, decreased, whereas forest edge-dependent species, Yellow-throated Bunting and Siberian Meadow Bunting, increased. The increase in omnivores in summer, may partly be explained by a considerable increase in the forest edge-dependent omnivore, Siberian Meadow Bunting.

There were several other expected effects of typhoon disturbance, which it was not possible to examine here in detail. The change of foliage height profile may have been related to declines in two generalist omnivores in the second winter (Pale Thrush and Red-flanked Bushrobin). These two species often forage in the open forest understory (Seki 1998), and may have experienced difficulties in foraging beneath the increased ground vegetation after typhoon 9918 Bart, as has been reported for other understory species (Canterbury & Blockstein 1997; Tejeda-Cruz & Sutherland 2005). Modifications to breeding habitats after storms may also affect bird communities (Engstrom & Evans 1990; Greenberg & Lanham 2001; Jones et al. 2001; Penteriani et al. 2002), and the increase in the Japanese Bush Warbler in the second summer following typhoon 9918 Bart might have been due to breeding habitat modification, as this species has a narrow nest site preference for dwarf bamboo thickets (Nakamura & Nakamura 1995), and the increase in dwarf bamboo after the typhoon may have provided additional breeding habitat for this species.

The bird community in the warm temperate forest at the study site showed clear seasonality not only in abundance, but also in the composition of dietary and foraging guilds. These guilds differed in their responses to environmental changes resulting from the typhoon's disturbance. Consequently, the same disturbance event appeared to have very different (and opposing) effects on total bird abundance in winter and in summer through the seasonal change in the bird community.

ACKNOWLEDGMENTS

I thank Kazuto Kawakami, Akira Endo, Tsuneaki Yabe, Norio Sahashi, Teruaki Hino, and Tamotsu Sato for helpful discussion. I also thank Masashi Murakami, Mark Brazil and two anonymous referees for their useful comments.

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Appendix 1. Bird species recorded during the study periods. Categorization of status at the study site was made into 5 types due to observation; resident (R), summer visitor (S), winter visitor (W), irregular or passage visitors (I), and resident plus winter visitor (R+W). Scientific and English Names follow Ornithological Society of Japan (2000).

English Name	Scientific Name	Status	English Name	Scientific Name	Status
Falconiformes			Passeriformes (continued)		
Northern Goshawk	*Accipiter gentilis*	I	Brown Thrush	*Turdus chrysolaus*	I
Japanese Sparrowhawk	*Accipiter gularis*	I	Pale Thrush	*Turdus pallidus*	W
Northern Sparrowhawk	*Accipiter nisus*	I	Eye-browed Thrush	*Turdus obscurus*	I
Common Buzzard	*Buteo buteo*	I	Dusky Thrush	*Turdus naumanni*	W
Peregrine Falcon	*Falco peregrinus*	I	Red-billed Liothrix	*Leiothrix lutea*	I
Galliformes			Shot-tailed Bush Warbler	*Urosphena squameiceps*	S
Chinese Bamboo Partridge	*Bambusicola thoracica*	R	Japanese Bush Warbler	*Cettia diphone*	R
Common Pheasant	*Phasianus colchicus*	R	Arctic Warbler	*Phylloscopus borealis*	I
Charadriiformes			Eastern Pale-legged Leaf Warbler	*Phylloscopus borealoides*	I
Eurasian Woodcock	*Scolopax rusticola*	W	Eastern Crowned Leaf Warbler	*Phylloscopus coronatus*	I
Columbiformes			Goldcrest	*Regulus regulus*	W
Oriental Turtle Dove	*Streptopelia orientalis*	R	Narcissus Flycatcher	*Ficedula narcissina*	S
Japanese Green Pigeon	*Sphenurus sieboldii*	I	Blue-and-white Flycatcher	*Cyanoptila cyanomelana*	I
Cuculiformes			Brown Flycatcher	*Muscicapa dauurica*	I
Oriental Cuckoo	*Cuculus saturatus*	I	Black Paradise Flycatcher	*Terpsiphone atrocaudata*	S
Little Cuckoo	*Cuculus poliocephalus*	S	Long-tailed Tit	*Aegithalos caudatus*	R
Strigiformes			Varied Tit	*Parus varius*	R
Ural Owl	*Strix uralensis*	R	Great Tit	*Parus major*	R
Apodiformes			Japanese White-eye	*Zosterops japonicus*	R+W
White-rumped Swift	*Apus pacificus*	I	Siberian Meadow Bunting	*Emberiza cioides*	R
Piciformes			Yellow-throated Bunting	*Emberiza elegans*	W
Japanese Green Woodpecker	*Picus awokera*	R	Black-faced Bunting	*Emberiza spodocephala*	W
Japanese Pygmy Woodpecker	*Dendrocopos kizuki*	R	Grey Bunting	*Emberiza variabilis*	W
Passeriformes			Brambling	*Fringilla montifringilla*	W
Barn Swallow	*Hirundo rustica*	S	Oriental Greenfinch	*Carduelis sinica*	W
House Martin	*Delichon urbica*	I	Eurasian Siskin	*Carduelis spinus*	I
Grey Wagtail	*Motacilla cinerea*	I	Eurasian Bullfinch	*Pyrrhula pyrrhula*	I
Japanese Wagtail	*Motacilla grandis*	I	Yellow-billed Grosbeak	*Eophona migratoria*	I
Olive-backed Pipit	*Anthus hodgsoni*	W	Masked Grosbeak	*Eophona personata*	W
Ashy Minivet	*Pericrocotus divaricatus*	W	Hawfinch	*Coccothraustes coccothraustes*	W
Brown-eared Bulbul	*Hypsipetes amaurotis*	R+W	Eurasian Tree Sparrow	*Passer montanus*	R
Bull-headed Shrike	*Lanius bucephalus*	W	Grey Starling	*Sturnus cineraceus*	W
Japanese Robin	*Erithacus akahige*	I	Eurasian Jay	*Garrulus glandarius*	I
Red-flanked Bushrobin	*Tarsiger cyanurus*	W	Rook	*Corvus frugilegus*	W
Daurian Redstart	*Phoenicurus auroreus*	W	Carrion Crow	*Corvus corone*	R
White's Thrush	*Zoothera dauma*	W	Jungle Crow	*Corvus macrorhynchos*	R