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SPECIAL FEATURE Interspecific segregation and attraction in forest birds

The effect of a typhoon on the flocking and foraging behavior of tits.

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Abstract A typhoon, that struck Kyushu, the southernmost of the four main islands of Japan, in September 1999, causing extensive wind damage to forests, was found to have affected the flocking and foraging behavior of Varied *Parus varius* and Great Tits *P. major*. After the typhoon had passed, the tits tended to participate in mixed-species flocks and preferred to forage in the lower parts, rather than in the upper parts, of the trees. Also the proportion of plant products in the diet of the Varied Tit was reduced. The population and average flock size of the tits, however, remained stable even after the typhoon. The abundance of plant products as food resources remained unchanged despite severe damage to the trees, but the vegetation cover was reduced, which probably increased the predation risk. The increase of mixed-species flocking may have resulted from the increased risk of predation; mixed-species flocking is thought to increase vigilance and foraging efficiency while not increasing intraspecific competition. Changes in diet and preferred foraging sites were also consistent with the increased predation risk hypothesis. We conclude that the changes in foraging and flocking behavior after the typhoon were mainly due to the increased predation risk caused by the reduced vegetation cover.

Key words Foraging site, Forest disturbance, Tit, Typhoon, Winter flocking

Disturbance by storms is among the most important 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, both directly as a result of the stress of storms and indirectly as a result of habitat modification (Askins & Ewert 1991; Lynch 1991; Waide 1991; Wunderle et al. 1992). Although many studies have reported on the population dynamics of birds after storms, little attention has been paid to their behavioral response.

In Kyushu, the southernmost of the four main islands of Japan, typhoons are the most significant agent of forest disturbance (Yamamoto 1992). The passage of a powerful typhoon through Kyushu in 1999 provided us with a rare opportunity to document the effects of a storm on avian behavior. The aim of this paper is to describe the effects of this severe typhoon on the flocking and foraging behavior of the Varied Tit *Parus varius* and the Great Tit *P. major*. Various factors affecting avian flocking and foraging behavior previously have been revealed, including: food abundance (Berner & Grubb 1985; Székely et al. 1989; Kubota & Nakamura 2000), weather conditions (Ekman 1984; Grubb 1987; Nakamura & Shindo 2001), inter- and intraspecific competition (Ekman 1987; Alatalo & Moreno 1987), abundance of congeneric species (Matthysen 1990), predator abundance (Suhonen 1993; Kullberg 1998), and the distribution of protective cover (Krams 1996). Despite the number of these studies, few have examined the effects of storms. To reveal the impact of the typhoon we compared the diets, foraging heights, and mixed-species flock attendance of the two species between the winters preceding and following the typhoon.

STUDY AREA AND METHODS

The study was carried out at Tatsutayama Experimental Forest in Kumamoto, Kyushu, Japan (32°49′N, 130°44′E, 28.4 ha, 48–152 m asl). Tatsutayama is an isolated hill forest area of about 450 ha,

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and the Experimental Forest is located on the southwestern slope of the hill. It is mostly covered with secondary evergreen broad-leaved forests 40–50 years of age, with some small coniferous plantations. The dominant tree species in this secondary forest is *Castanopsis cuspidata*, with an average height of about 17 m.

On 24 September 1999, a severe typhoon (9918 Bart) struck Kyushu and its eye passed within 40 km of the Experimental Forest moving at 40 km h^{-1}, with a pressure at the eye of 945 hPa. At the Kumamoto Local Meteorological Observatory, 2.5 km west of our study site, a wind speed of over 10 m s^{-1} was recorded for seven hours, with a maximum speed of 49.0 m s^{-1} (Japan Meteorological Agency 1999).

To examine the structural damage caused to trees by typhoon 9918 Bart, we established five 2 m×50 m transects within which we measured all the trees above breast height, and categorized the trees into three groups: 1) Sound; mostly healthy with slight or little defoliation; 2) Injured; trunk broken, trunk leaning, trunk down, limbs broken, or severely defoliated, and 3) Dead; died within two years of the typhoon.

To examine the effect of the typhoon on the population and flocking behavior of tits, we conducted annual bird censuses from 15 November to 31 December, from 1996 to 1999. Since the number of tits and their flocking and foraging behavior change continuously throughout the year, we confined the study to this short period when the social organization of tits is relatively stable (Saitou 1978; Gosler 1993; Kubota & Nakamura 2000). Moreover, since we could not find an appropriate control site, we compared the data sets from the four years defining the three years 1996-1998 as control years and 1999 as a disturbed year. To reduce the possibility of misidentifying the 'among-year-fluctuation' to be an effect of the typhoon, we regarded only those values in 1999 that were significantly different from those of the other three years, as having been disturbed by the typhoon. Although some typhoons affect our study site every year, no severe typhoons with maximum wind speeds of over 40 m s^{-1} were recorded in the control years nor during the five years prior to the research.

An elliptical, 3.8 km, census route was established in the study site, and this was surveyed six times each year between 0730 and 1030. The species and number of all birds observed within 25 m on either side of the route were recorded. We carefully avoided repeated counts of the same flock. Since the vegetation was not dense in our study site, we assumed that detectability within 25 m of the transect line was high and constant, and that the number of tits recorded within the area reflected their relative densities.

Each tit encountered was categorized as either participating in a mixed-species flock, in a mono-specific flock, or as being solitary. Three criteria were used to define a flock: (1) all members remain within about 20 m of each other; (2) flock members remain together for at least three minutes, and (3) members move at least 30 m in the same direction. When more than two birds of two species were associating together, they were defined as a mixed-species flock, following Bell's definition (1986).

In our study area, in addition to Paridae other species were also recorded as participating in mixed-species flocks. These included: Long-tailed Tit *Aegithalos caudatus*, Japanese White-eye *Zosterops japonicus*, Japanese Pygmy Woodpecker *Dendrocopos kizuki*, Goldcrest *Regulus regulus*, Ashy Minivet *Pericrocotus divaricatus*, Red-flanked Bushrobin *Tarsiger cyanurus*, and Japanese Bush Warbler *Cettia diphone*.

It was not possible to determine the social organization of the Varied and Great tits in detail, since individual were not marked, therefore, we used the term 'mono-specific units' to describe the basic social organization that included solitary individuals, mono-specific flocks, and the same species members belonging to mixed-species flocks. Mixed-species flock attendance rate was calculated for each species as the proportion of individuals attending the mixed-species flocks in relation to the total number of individuals observed.

To examine the effects of abiotic factors, we compared the weather parameters on census dates in the control and disturbed years, daily average temperature and wind velocity, recorded at the Kumamoto Local Meteorological Observatory. These data were provided by the Japan Meteorological Agency.

We recorded the diet and the foraging heights where successful foraging attempts by tits were observed, from November to January each year. Foraging heights were divided into four categories: (1) upper layer (>12 m), (2) middle layer (6–12 m), (3) lower and shrub layers (0–6 m), and (4) on ground. Unfortunately, we could not divide these observations according to whether or not birds attended mixed-species flocks, because we recorded foraging behavior independently of the bird censuses.

The abundance of acorns and other seeds was estimated using litter traps. Ten round traps, each with an opening of 0.58 m^2, were placed in the *C. cuspidata* forest and we collected the contents over the three winter month of November, December and January. We sorted out seeds and mature acorns from the contents, oven-dried (70°C, 72 h) and weighed them. Small immature acorns were excluded from the abundance measurement, since tits seldom fed on them (Higuchi 1975).

We used the Kruskal-Wallis test to analyze the flock size data. To evaluate the differences among groups, we employed Dunn's procedure following Zar's manual (1999). We simply used chi-square test (contingency table) to analyze if the mixed-species flock attendance, foraging sites, and food items were independent of year, because our sample sizes were large enough to use this test without correction in most cases. When those variables were not independent of year, we then evaluated the contribution of each cell of the contingency tables using adjusted residuals (d_{ij}), which are approximate to z scores (Everitt 1977).

RESULTS

1) Disturbance by the typhoon

After the typhoon passed, 8.4% of the trees above breast height died and 28.2% were severely injured (their limbs and/or trunks were broken, or they were uprooted; see Table 1). The wind damage to the canopy was greater than that to the sub-canopy, 13.6% of the canopy trees (with a diameter at breast height of over 20 cm) died and 72.7% were severely damaged (Table 1).

Most of the trees in our study site were extensively defoliated by the strong typhoon winds, and annual litter fall in 1999 was 1.3- to 2.0-fold greater than during the three years prior to the typhoon (Sato unpublished). As a result of this destruction, the average canopy cover was reduced from 95.4% to 87.2% (Saitou, S. personal communication). We have only limited information on the winter predation risk relating to this decrease of cover. The mortality of young birds, however, was higher during the breeding season following the typhoon than in the preceding seasons. For example, 52.3% of young Great Tits disappeared within two weeks after fledging in 2000, whereas only 28.6% had disappeared in 1997 (chi-square test, $\chi^2=5.55$, df=1, P=0.019). We also observed several attacks on family flocks of Great Tits in 2000, but not in other years. These attacks included three by Jungle Crows *Corvus macrorhynchos* (one was successful), and one successful attack by a Japanese Lesser Sparrowhawk *Accipiter gularis* (Seki unpublished).

Despite the severity of the habitat modification resulting from the passage of the typhoon, the differences among years were not significant for either temperature or wind velocity (Table 2).

2) Number of tits

The number of individual Varied Tits recorded did not differ significantly among years (Table 3). The number of Great Tits observed in the three years 1997, 1998 and 1999, did not differ significantly, although the number of birds seen in 1996 differed significantly from the number in 1999 (Dunn's procedure, 1996 vs 1999, $Q=3.50$, $P<0.005$; 1997 vs 1999, $Q=1.00$, $P>0.50$; 1998 vs 1999, $Q=0.65$, $P>0.50$).

3) Size and composition of flocks

Neither the size of mono-specific units, nor the size of mixed-species flocks containing each species of tit, differed among the four years for either tit species

Table 1. Structural damage to trees in the study area caused by typhoon 9918 Bart. Figures show the number of trees in each category.

DBH class (cm)	<10	10–20	20–30	30–40	>40
Sound	226	9	5	1	
Injured	61	14	24	6	2
Dead	18	8	4	2	

Table 2. Weather parameters on census dates recorded at the Kumamoto Local Meteorological Observatory (mean±SD). Data were provided by the Japan Meteorological Agency, through the database of the Computer Center for Agriculture, Forestry and Fisheries Research.

	1996	1997	1998	1999	F	P
Temperature (°C)	7.7±3.3	9.1±4.9	8.4±2.4	5.8±3.9	0.83	0.50
Wind velocity (m/s)	1.6±0.3	1.9±0.6	1.6±0.2	2.1±0.4	2.24	0.12

Table 3. Comparison of observed number of individuals and the size of flocks in the control years and in the year disturbed by the typhoon (mean±SD).

Species		Year	Number of individuals (per census)	N[1]	Size of mono-specific units[2]	N[3]	Size of mixed-species flocks[4]	N[3]
a) Varied Tit	Control years	1996	23.8±8.6	6	2.6±1.8	55	16.7±9.8	10
		1997	24.2±3.6	6	2.1±1.1	69	8.1±5.2	14
		1998	18.2±3.2	6	2.1±1.2	52	9.4±6.0	11
	Disturbed year	1999	18.8±3.5	6	1.9±0.8	59	11.0±10.0	30
	Kruskal-Wallis test (df=3)		Hc=6.48 P=0.09		Hc=4.77 P=0.19		Hc=5.15 P=0.16	
b) Great Tit	Control years	1996	6.5±1.4*	6	1.5±0.8	26	11.9±9.9	14
		1997	15.3±3.7	6	1.7±0.8	54	9.1±5.2	19
		1998	16.2±1.7	6	1.9±1.0	51	12.6±9.6	17
	Disturbed year	1999	19.3±6.2	6	2.0±1.0	59	10.6±9.7	36
	Kruskal-Wallis test (df=3)		Hc=14.04 P=0.003		Hc=5.65 P=0.13		Hc=1.32 P=0.72	

1 Frequency of census
2 We used the term 'mono-specific units' to mean a basic social organization, including solitary individuals, mono-specific flocks, and the same species members belonging to mixed-species flocks.
3 Number of observed units or flocks each year
4 Size of mixed-species flocks containing each species of tit that also include the number of species other than tits: Long-tailed Tit, Japanese White-eye , Japanese Pygmy Woodpecker, Goldcrest, Ashy Minivet, Red-flanked Bushrobin, and Japanese Bush Warbler.
* Significant difference from 1999 (P<0.05, Dunn Procedure).

Table 4. Mixed-species flock attendance rates (%) in the control years and in the year disturbed by the typhoon.

	Control years						Disturbed year		χ^2-test		
	1996	N[1]	1997	N[1]	1998	N[1]	1999	N[1]	df	χ^2	P
Tits											
Varied Tit	30.8	143	23.4	145	17.4	109	52.2	113	3	37.26	<0.001
Great Tit	59.0	39	31.9	92	36.1	97	68.1	116	3	38.45	<0.001
Long-tailed Tit	50.8	252	48.3	201	56.6	234	91.1	169	3	89.00	<0.001
Other species											
Japanese White-eye	10.4	554	12.8	240	11.7	358	35.3	292	3	91.63	<0.001
Japanese Pygmy Woodpecker	23.3	47	34.0	60	34.8	46	51.7	58	3	10.51	0.015
Goldcrest	22.2	2	0.0	9	57.1	14	100.0	11		–	–
Ashy Minivet	0.0	19	10.5	20	0.0	12	13.3	15		–	–
Red-flanked Bushrobin	0.0	44	2.3	42	2.2	45	5.7	35		–	–
Japanese Bush Warbler	0.0	55	0.0	77	1.3	76	0.0	85		–	–

1 Sample size (N) shows the total number of individuals observed each year.

(Table 3).

The mixed-species flock attendance rate of the Great Tit was always higher than that of the Varied Tit within each year, even in the disturbed year (Table 4). The mixed-species flock attendance rate in 1999 was higher than in the three control years, not only for both *Parus* species but also for the Long-tailed Tit, the Japanese White-eye and the Japanese Pygmy Woodpecker (Table 4). The results in 1999 contributed most to the dependence on year in all these

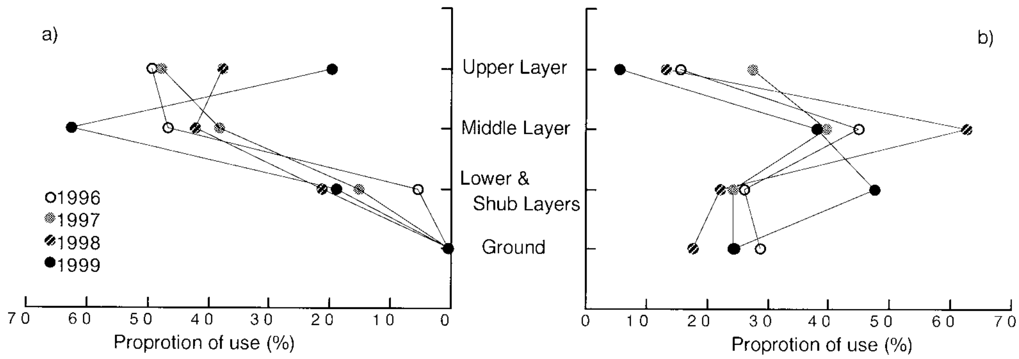

Fig. 1. The foraging heights of a) Varied Tit and b) Great Tit in the control years and in the year disturbed by typhoon 9918 Bart. The observed frequency of feeding attempts each year is shown in Table 5.

species (adjusted residuals, Varied Tit, $d_{mixed, 1999}$=5.65, P<0.001; Great Tit, $d_{mixed, 1999}$=5.45, P<0.001; Long-tailed Tit, $d_{mixed, 1999}$=9.06, P<0.001; Japanese White-eye, $d_{mixed, 1999}$=9.54, P<0.001; Japanese Pygmy Woodpecker, $d_{mixed, 1999}$=2.92, P=0.004). For the other four species, we could not perform statistical analyses, because the number of individuals participating in mixed-species flocks was too small. Although we do not have quantitative data on the leader-follower relationships in the mixed-species flocks, if Long-tailed Tits were present they usually led the flock. In those flocks without Long-tailed Tits, we did not find any tendency for the Varied Tit or the Great Tit to be the leader (Seki, pers. obs.).

4) Foraging heights

Varied Tits were only observed foraging in trees and never on the ground during the study period (see Fig. 1). The observed frequency of each forest layer used was not independent of year in the Varied Tit (chi-square test, χ^2=27.31, df=6, P=0.001). After the typhoon's passage, the Varied Tit foraged significantly less in the upper layer and significantly more in the middle layer instead (adjusted residuals, upper layer, $d_{upper, 1999}$=−4.48, P<0.001; middle layer, $d_{middle, 1999}$=3.29, P=0.001; lower and shrub layer, $d_{lower, 1999}$=1.47, P=0.14). The Great Tit also foraged less in the upper layer after the disturbance and shifted to the lower part of the trees, although the effect of year was not significant (chi-square test, χ^2=15.12, df=9, P=0.09).

5) Diet components

In our research area, plant materials accounted for 47.3 to 53.5% of the Varied Tit's diet in the control years, whereas the proportion of plant materials in the diet decreased to 30.1% in the disturbed year (Table 5). Since unspecified items were assumed to be invertebrates (on the basis of the foraging site), we divided their diet into two parts, plant diet, and non-plant diet. The observed frequency of each group foraged was not independent of year (chi-square test, χ^2=12.33, df=3, P<0.001), and the results in 1999 contributed most for the dependence on year (adjusted residuals, $d_{plant, 1999}$=−3.43, P<0.001).

The Great Tit also fed on plant products although the proportion was not high (Table 5). The Great Tit seldom ate acorns, probably because of physical constraints. In fact, we observed only two incidences of Great Tits eating acorns, in both cases they were broken due to drying. The diet composition of the Great Tit was independent of year during the study period (chi-square test, χ^2=1.09, df=3, P=0.78).

6) Plant abundance

The abundance of plants, especially acorns, was highly variable among years (Table 6). Although acorns and seeds were not abundant in 1999, the abundance was still greater than that of the previous winter, which was one of the control years undisturbed by severe typhoons.

DISCUSSION

We observed three changes in tit behavior after the severe disturbance caused by the typhoon. First, attendance rate in mixed-species flocks increased after the disturbance compared with the previous three years. Secondly, the proportion of plants in the Varied Tit's diet was reduced, although there was no change in the Great Tit's diet. Finally, the tits tended to prefer the lower part of the trees to the upper part as their foraging sites. The population and average flock size of the tits, however, were rather stable in spite of the

Table 5. Annual variation in the winter diet (%) of Varied and Great Tits from 1996-1998.

		Varied Tit				Great Tit			
		Control years			Disturbed year	Control years			Disturbed year
		1996	1997	1998	1999	1996	1997	1998	1999
Plant materials									
	Acorns	37.5	24.3	27.9	19.4	4.5	0.0	0.0	0.0
	Seeds	15.0	23.0	25.6	10.7	6.8	7.9	15.4	9.2
Non-plant materials									
Invertebrates	Caterpillars	12.5	10.8	14.0	11.7	20.5	15.8	19.2	20.0
	Pupae	2.5	5.4	0.0	4.9	2.3	18.4	7.7	4.6
	Spiders	1.3	1.4	2.3	1.9	2.3	10.5	7.7	9.2
	Lepidoptera(adults)	0.0	1.4	0.0	1.9	4.5	2.6	11.5	3.1
	Hemiptera	1.3	1.4	0.0	1.9	0.0	5.3	3.8	3.1
	Coleoptera(adults)	0.0	1.4	2.3	5.8	0.0	0.0	0.0	3.1
	Diptera(adults)	0.0	1.4	0.0	2.9	0.0	2.6	3.8	1.5
	Hymenoptera(adults)	0.0	0.0	0.0	0.0	2.3	0.0	0.0	1.5
	Other Invertebrates	12.5	5.4	7.0	8.7	31.8	10.5	11.5	12.3
Unspecified		17.5	24.3	20.9	30.1	25.0	26.3	19.2	32.3
Total number of items		80	74	43	103	44	38	26	65

Table 6. Abundance (kg ha^{-1}) of acorns and other seeds in the control years and in the year disturbed by the typhoon.

		Acorns	Other seeds
Control years	1996	456.77	1.66
	1997	75.92	1.91
	1998	1.64	1.34
Disturbed year	1999	4.38	1.43

extensive habitat modification.

Foraging and flocking decisions are very sensitive to biotic and abiotic environmental changes (Matthysen 1990); since small passerines suffer from energy shortages during the cold and short winter days (Jansson et al. 1981), they always face a trade-off between the benefit of efficient foraging and the cost of predation risk when they make behavioral decisions (reviewed in Lima & Dill 1990; Matthysen 1990; Suhonen et al. 1993). Based on previous studies dealing with wind disturbance (Askins & Ewert 1991; Engstorm & Evans 1990; Grant et al. 1997; Lynch 1991; Waide 1991; Wunderle et al. 1992), we had expected two major environmental changes: fluctuation of food abundance and the decrease of vegetation cover.

Fluctuations in food abundance, however, are unlikely to have caused the behavioral changes in the present study. Although the strong typhoon winds in 1999 blew off large numbers of immature acorns and seeds (Sato unpubl.), the production of mature acorns and seeds during the following winter was still greater than that of poor crop years, such as 1998 (Table 6). The seed production of tree species in general is highly variable between years regardless of the effects of wind storms (Higuchi 1975; Kelly 1994). In 1998, Varied Tits selectively ate acorns despite their low abundance, but did not do so in 1999. Neither Great Tit nor Varied Tit increased their mixed-species flock attendance rate in 1998, but in 1999 they did. The decrease of plant products after the typhoon seems unlikely to be the cause of behavioral changes of tits. Furthermore, potential invertebrate prey for tits did not markedly increase or decrease even in the disturbed winter. Increases in invertebrates, which might have caused the Varied Tit to alter its diet, have often been reported after storms, but usually occur from spring following the damage (Thompson 1983; Furuta et al. 1984). Decreases in invertebrates, which might happen after canopy destruction and thus lead to mixed-species flocking, could not have been so severe in the study area, because Varied Tits risked shifting their diet from plant products to invertebrates in the disturbed winter.

Reduced cover could have caused the observed behavioral changes as a result of the increased risk of predation (Engstorm & Evans 1990; Thiollay 1997;

Grant et al. 1997). The reduced degree of vegetation cover was observed also in our study area, and it continued throughout the winter, since refoliation and sprouting could not proceed so rapidly in warm temperate forests (Bellingham et al. 1996). Although we have only limited information on the winter predation risk, the increased mortality of young during the breeding season after the typhoon would support our increased predation risk assumption.

Higher predation risk increases the mixed-species flock attendance rate (Székely et al. 1989; Ekman 1989; Matthysen 1990; Suhonen et al. 1993), because heterospecific flocking is assumed to increase vigilance and foraging efficiency but does not increase intraspecific competition (reviewed in Lima & Dill 1990; Bednekoff & Lima 1998). Moreover, since individuals in heterospecific flocks are probably not influenced by long-term social bonds, interspecific associations are more sensitive than intraspecific associations to environmental changes (Matthysen 1990), such as the disturbance caused by a typhoon. Our findings, that mixed-species flocking increased once vegetation cover had been reduced, were consistent with the increased predation risk hypothesis. The average size of mixed-species flocks in 1999 did not increase in spite of the increased mixed-species flock attendance rates, presumably because of the smaller size of mono specific units of the Long-tailed Tit, nuclear species for mixed-species flocks (averaging 7.4 in 1999 and 7.9–12.0 during 1996–98).

Predation risk also affects the diet of prey species. Numerous studies have demonstrated that the presence of predators increases the proportions of prey items found and consumed in a safer place with a safer method (Lima 1988a; Lima 1988b; Suhonen 1993; Suhonen et al. 1993; Krams 1996; Kullberg 1998, to name a few). The Varied Tit preferred the acorns of *C. cuspidata* before the disturbance, since other species did not take it in spite of its high energetic efficiency. However, acorns have some disadvantages compared to invertebrates in their degree of safety from predators: (1) The Varied Tit is less vigilant while handling them since its ability to detect a predator is greater when it is raising its head (Lima et al. 1999); (2) predators might be able to locate the tit on the basis of its loud hammering noise (Székely et al. 1989); and (3) unspoiled acorns are distributed in the outer parts of trees where the vegetation cover was destroyed most severely. We suggest that the Varied Tit gave up foraging on acorns under the decreased vegetation cover, as a trade-off between efficient foraging and safety from predators while foraging on acorns. Furthermore, this shift in the diet could also be attributed to the increased mixed-species flock attendance rate of the Varied Tit, since the benefit of copying other species might be greater when they feed on cryptic invertebrates (Waite & Grubb 1988). The Great Tit, in contrast, did not show any changes in its diet, which might be because its diet consisted of invertebrates that are easier to handle than plant products, and because they are distributed in various parts of the trees.

The changes in the preferred foraging heights after the typhoon might also be due to the predation risk. The reduction of cover was most notable in the upper layer, which the tits avoided after the disturbance. However, the new foraging heights, where the tits appeared after the typhoon, differed between the Varied and Great tits. There are several possible reasons for this difference, such as inter-specific relationships (Nakamura & Shindo 2001) and the distribution of food resources, although we cannot discuss these in detail as we know little about the quality of each foraging substrate, the dominant-subordinate relationship in the mixed-species flocks, or the movement of leading species.

We therefore conclude that the changes in foraging and flocking behavior after the typhoon were mainly due to the increased predation risk caused by reduced vegetation cover.

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