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Tree species preferences of insectivorous birds in a Japanese deciduous forest: the effect of different foraging techniques and seasonal change of food resources

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Abstract I examined the effects of arthropod abundance and of bird foraging techniques on the tree species preferences of seven insectivorous bird species in a temperate deciduous forest. It is hypothesized that bird species with a wide range of foraging techniques respond more flexibly to the spatial distribution and seasonal change of prey than those with specialized foraging techniques. This hypothesis was supported by the fact that tits, bird species with a wide range of foraging techniques, changed their techniques when foraging in tree species with different foliage structures. They also used various tree species in late summer when food requirements increased owing to the addition of nestlings and fledglings. Bird species with a narrow range of foraging techniques, such as flycatchers and white-eyes, did not change their techniques among tree species and had strong tree species preferences in all research periods.

Key words Foliage structure, Prey abundance, Tree species preference, Variety of foraging technique

Tree species diversity is one of the most important habitat factors determining bird species diversity in temperate forests, because diverse composition of tree species should facilitate the coexistence of different species of birds (Holmes et al. 1979; Rice et al. 1984; Hino 1985). However, the mechanism of coexistence has not been sufficiently understood. Although many studies have shown different use of tree species among insectivorous birds (e.g., Hartley 1953; Nakamura 1970; Morse 1978; Recher et al. 1991), most such studies have not surveyed the availability of food for birds on different tree species (but see Holmes & Robinson 1981; Diaz et al. 1998; Hino et al. 2002). The abundance and distribution of prey, and the foliage structure, which vary among tree species, influence prey detectability and accessibility by birds (Holmes & Schultz 1988). Thus, the prey availability for each bird species must be determined separately for each tree species. Since different tree species provide different foraging opportunities for birds, tree species composition within a forest should influence bird species composition and diversity (Holmes & Schultz 1988).

Prey abundance for birds varies among tree species and changes temporally during the breeding season (Feeny 1970; Nager & van Noordwijk 1995; Dias & Blondel 1996; Murakami 1998). Foraging techniques, determined by morphological characteristics of each bird species (Moreno & Carrascal 1993; Carrascal et al. 1995), affect bird preferences for foraging habitat (Nakamura 1978; Holmes and Schultz 1988; Hino et al. 2002). Different foliage structure among tree species often requires foraging birds to use different foraging techniques (Whelan 1989). Under these circumstances, we hypothesize that birds with a variety of foraging techniques can respond flexibly to temporal change and spatial distribution of food abundance. So far, few studies have examined this hypothesis (but see Hino et al. 2002; Murakami 2002).

This study examined the use of tree species and the foraging techniques of seven forest bird species in temperate deciduous forest. Temperate deciduous forests are most appropriate for the study of tree species preferences of birds because the number of

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tree species is not as high as in tropical forest and not as low as in coniferous boreal forest. I analyzed how seasonal changes in tree species preferences of birds were affected by their foraging techniques, by prey abundances and by the foliage structure of trees.

MATERIALS AND METHODS

1) Study site

This research was conducted in the experimental forest of the Hokkaido Research Center, the Forestry and Forest Products Research Institute, located in Sapporo, Japan (42°59′N, 141°23′E). A 9 ha-study area was established in a secondary deciduous broadleaved forest, which had been burned about 70 years ago. The vegetation was surveyed in fifteen 25m-square plots selected randomly in the study area. Species, number of individuals, and diameter at breast height (DBH) were recorded for all trees. Tree species composition was calculated as the percentage of basal area given by DBH. The dominant tree species are Japanese White Birch (*Betula platyphylla*, 46.2%), Oak (*Quercus mongolica* v. *grosseserratus*, 13.7%), Casterarealia (*Kalopanax pictus*, 10.0%), Printed Maple (*Acer mono*, 5.0%), Japanese Linden (*Tilia japonica*, 5.0%) and Alder (*Alnus hirsuta*, 4.3%). The understory is dominated by a high density of dwarf bamboo (*Sasa senanensis* and *S. kurilensis*) 0.5–2 m in height.

Budding of most trees starts in early May. Research was conducted from 21 May to 5 July in 1992 and from 22 May to 19 June in 1993. Five research periods of two weeks each were established for bird observations and prey sampling: 92-1 (21 May–5 June), 92-2 (6 June–20 June), 92-3 (21 June–5 July) in 1992; 93-1 (22 May–5 June), 93-2, (6 June–19 June) in 1993.

2) Bird foraging

The target species were seven insectivorous bird species. These were three resident species: Great Tit (*Parus major*), Marsh Tit (*P. palustris*) and Long-tailed Tit (*Aegithalos caudatus*), and four migrant species appearing in May: Japanese White-eye (*Zosterops japonica*), Narcissus Flycatcher (*Ficedula narcissina*), Eastern Crowned Leaf Warbler (*Phylloscopus coronatus*) and Brown Flycatcher (*Muscicapa dauurica*). Observations of Marsh Tits may have included Willow Tits (*Parus montanus*), which were very low in abundance, because those two species are difficult to distinguish in the field. The data on fledglings were excluded from the analysis.

I observed bird foraging behavior through binoculars (8–16 times zoom) from 0500 to 1000 except on rainy days or on days with strong wind. When a foraging bird was encountered, I followed it as long as possible, and recorded the tree species it visited and its foraging techniques. Foraging techniques were classified into three types: perch-gleaning (gleaning prey from leaves or branches while perching on branches); hang-gleaning (taking prey from leaves or twigs by hanging upside down from twigs or leaves); and hovering. In this study, one tree individual was regarded as one patch for foraging. Even if birds searched but did not capture prey on a tree during the observation, thus, the datum was dealt with as one sample of use of the tree species. Even if a bird foraged many times successively on the same tree, the datum was dealt with as one sample. When a bird foraging on a particular tree species flew to the same tree species less than 3 m away, or with and overlapping crown, or when a bird being followed was lost to sight for a few seconds in foliage (when no other conspecific birds were found nearby), the datum was also dealt with as one sample. In contrast, all data relating to foraging techniques were dealt with as independent samples even when foraging occurred successively on the same tree. No more than 10 samples of foraging technique observations were taken from each individual bird. The data included both feeding nestlings or fledglings and foraging for themselves. To avoid bias from repeated observations of the same individuals, I collected the data while walking steadily within the study area.

The preferences of birds for each tree species were calculated using Ivlev's electivity index (Ivelv 1955): $E=(p_i-r_i)/(p_i+r_i)$, where p_i represents the proportions of the ith tree species used by a particular bird species and where r_i is the proportion of tree species composition occupied by the ith tree species in the study area. Following Holmes and Robinson (1981), the 'tree preference index' was obtained as a sum of the percentage deviations of bird use from the tree species composition for six dominant species (*B. platyphylla*, *Q. mongolica*, *K. pictus*, *A. mono*, *T. japonica*, *A. hirsuta*). This index shows that the higher the value is, the more specialized the bird is in tree species use. The similarity in tree species use between two bird species was calculated with Pianka's index (Pianka 1973):

$$\alpha_{jk}=\sum_i p_{ij}\cdot p_{ik}\Bigg/\left(\sqrt{\sum_i (p_{ij})^2}\ \sqrt{\sum_i (p_{ik})^2}\right),$$

where p_{ij} and p_{ik} are the proportions of the ith tree species used by the jth and the kth bird species, respectively. The similarity between tree species use by birds and tree species composition in the study plot was also calculated using Pianka's index. The cluster analyses were performed using Mountford's method (Mountford 1962). The variation in foraging techniques was shown using Shannon's H' (Shannon & Weaver 1949): $H'=-\sum q_j \log_2 q_j$, where q_j is the proportion of the jth foraging technique.

3) Arthropod sampling

Spiders and insects were searched for, counted and measured, at 1–2 m in height in four species of trees (*A. mono*, *A. hirsuta*, *Q. mongolica* and *T. japonica*) in 1992 and six species (addition of *B. platyphylla*, and *K. pictus*) in 1993. Each sample consisted of 400 leaves with branches and twigs for five of these tree species, with the exception of *K. pictus* of which 50 leaves were sampled owing to their very large size. Seven units were sampled for each tree species in all research periods in 1992, ten in 93-1, and nine in 93-2. Dry mass (W, mg, 60°C, 48 h) of arthropods was estimated from the body length (L, mm) with the following equation: $W=0.12\,L^{1.64}$ ($r=0.83$, $P<0.001$, $N=78$), which was determined based on part of the samples. Leaf areas were measured (using a digitizer) for 25 leaves for each tree species in July to calculate the arthropod dry mass per 1 m^2 leaf area.

4) Statistical analyses

Chi-square tests were conducted to reveal differences in tree species use among bird species during each research period. Some tree species were combined to make expected frequencies large enough for chi-square tests. Chi-square tests and Fisher's exact probability tests with multiple comparison methods were conducted to compare the frequencies of the tree species used by a bird species with the frequencies expected from tree species composition during each research period. Chi-square tests with multiple comparison methods were also conducted to reveal the differences in foraging techniques used by each bird species between tree species. Mantel-Haenszel tests were conducted to detect similarities of relative frequencies of foraging techniques on different tree species among bird species. The arthropod dry mass per 1 m^2-leaf area data were log-transformed to reduce skewness for ANOVA. Two-way ANOVAs were conducted to reveal the seasonal changes in arthropod abundances on different tree species (factor=period, tree species). One-way ANOVAs were conducted to reveal the differences in arthropod abundances among tree species during each period (factor=tree species). Spearman's rank correlation tests were conducted to reveal the relationship between arthropod abundances and selectivity of tree species for each bird species during each research period. Sequential Bonferroni methods (Rice 1989) were used for multiple comparisons in nonparametric tests and Fisher's PLSDs were used in ANOVA. Statistical significances were evaluated at $P<0.05$ except for correlation analyses. $P<0.1$ was considered as the significance level for correlation analyses owing to the small sample sizes involved (4 or 6).

RESULTS

1) Tree species preferences of foraging birds

The uses of tree species differed significantly among bird species during all research periods (Table 1). In the 92-1 period, *A. mono* was preferred by three species of tits and *Q. mongolica* was preferred by Great Tit, but *B. platyphylla* was avoided by most species of birds. In the 92-2 period, neither preference nor avoidance for tree species was shown by any bird species except for Eastern Crowned Leaf Warbler preferring *Q. mongolica*. In the 92-3 period, *K. pictus* was preferred by Marsh Tit and Eastern Crowned Leaf Warbler, but *B. platyphylla* was avoided by Marsh Tit and Japanese White-eye. In the 93-1 period, *A. mono* was preferred by three species of tits and *Q. mongolica* was preferred by Eastern Crowned Leaf Warbler, Japanese White-eye and Narcissus Flycatcher, but *B. platyphylla* was avoided by all species of birds. In the 93-2 period, *B. platyphylla* was avoided by Great Tit and Narcissus Flycatcher. On the whole, the preferred or avoided tree species appeared to be consistent for each bird species during each research period, although the use of tree species differed significantly among bird species (Table 1).

The tree preference index for each bird species was compared between the first (92-1, 93-1) and the later research periods (92-2, 92-3, 93-2). This index decreased for Long-tailed, Great, and Marsh tits, but increased or remained unchanged for the Narcissus Flycatcher in both years (Table 2). This index increased for Eastern Crowned Leaf Warbler in 1992 but de-

Table 1. Preferential use of tree species by foraging bird species and tree species composition in the study area. + or − represent differences between the percent of each bird species using a tree species and the percent of the tree species composition of the same tree species . Some bird species were not shown in each period owing to sample size being too small for analysis. AM=*Acer mono*, AH=*Alnus hirsuta*, QM=*Quercus mongolica*, TJ=*Tilia japonica*, BP=*Betula platyphylla*, KP=*Kalopanax pictus.*

	Tree species						Number of observations	** χ^2 test
	AM	AH	QM	TJ	BP	KP		
92-1 period								
Long-tailed Tit	+22.1*	+4.1	+8.3	+1.8	−32.6*	−4.9	59	χ^2=59.0
Great Tit	+25.8*	−2.9	+16.6*	−0.1	−27.2*	−5.1	142	df[1)]=20
Marsh Tit	+8.5*	+1.6	+9.7	−1.3	−25.0*	−5.1	186	P<0.001
Eastern Crowned Leaf Warbler	+6.5	−0.5	+20.9	−3.1	−9.7	−6.2	52	
Narcissus Flycatcher	+6.7	+2.2	+16.2	−3.7	−22.8*	+1.7	77	
92-2 period								
Long-tailed Ti	+4.5	+5.2	+19.6	−5.0	−22.4	−10.0	21	χ^2=33.8
Great Tit	+9.6	+3.5	−0.3	−3.1	−9.3	−4.2	103	df[2)]=12
Marsh Tit	−3.4	−1.0	−2.2	−3.4	−6.3	−8.4	61	P<0.001
Eastern Crowned Leaf Warbler	+2.5	−4.3	+26.3*	−2.5	−21.2	+2.5	40	
Narcissus Flycatcher	+7.9	+2.2	+18.6	+1.5	−29.7	−3.5	31	
92-3 period								
Long-tailed Tit	−5.0	−0.9	+7.0	+1.9	−8.9	−10.0	29	χ^2=55.1
Great Tit	+0.3	+2.7	−0.5	−3.2	−13.7	+11.1	114	df[3)]=15
Marsh Tit	−4.1	+2.1	+2.8	−3.2	−14.1	+20.3*	109	P<0.001
Eastern Crowned Leaf Warbler	−1.6	+6.0	−3.4	−5.0	−37.6*	+26.2*	58	
Japanese White-eye	−5.0	+2.8	+22.0	+2.1	−42.6*	+18.5	28	
Narcissus Flycatcher	+11.0	+3.7	+14.3	−1.0	−30.2	+10.0	25	
93-1 period								
Long-tailed Tit	+28.3*	−4.3	+19.6	+1.1	−34.1*	−10.0	33	χ^2=55.8
Great Tit	+18.3*	+1.9	+9.6	+4.6	−29.8*	−5.2	146	df[4)]=24
Marsh Tit	+17.8*	−2.4	+1.7	+6.1	−24.6*	−8.1*	162	P<0.001
Eastern Crowned Leaf Warbler	+10.1	−0.5	+25.9*	+2.5	−29.2*	−8.1	53	
Japanese White-eye	+11.7	−0.6	+34.4*	−1.3	−42.5*	−10.0	27	
Narcissus Flycatcher	−0.2	−0.7	+28.0*	+3.3	−33.1*	+6.7	84	
Brown Flycatcher	+10.4	−4.3	+20.9	−1.2	−15.4	+1.5	26	
93-2 period								
Great Tit	+9.3	+1.0	+5.1	+7.0	−16.1*	−1.0	133	χ^2=26.5
Marsh Tit	+5.1	−1.8	+8.1	−1.6	−8.4	−3.3	119	df[5)]=12
Eastern Crowned Leaf Warbler	+2.3	+0.6	+15.5	−0.1	−9.6	−2.7	41	P<0.001
Narcissus Flycatcher	+12.9	+11.1	+11.9	+2.7	−41.1*	+0.2	39	
Tree species composition (%)	5.0	4.3	13.7	5.0	46.2	10.0		

* P<0.05, comparisons of the tree species composition for each tree species and the use of same tree species for each bird species by each period and bird species (χ^2 test or Fisher's exact test with sequential Bonferroni method).
** Comparisons with use of tree species at each period.
[1–5)] Tree species categories were combined to make expected frequencies large enough for chi-square tests.
[1)] Six tree categories; AM, QM, TJ, BP, KP, AH+other tree species.
[2)] Four tree categories; AM, QM, BP, AH+KP+TJ+other tree species.
[3)] Four tree categories; QM, BP, KP, AM+AH+TJ+other tree species.
[4)] Five tree categories; AM, QM, TJ, BP, AH+KP+other tree species.
[5)] Five tree categories; AM, QM, TJ, BP, AH+KP+other tree species.

Table 2. Tree Preference Index during each period. Some bird species were not shown for each period owing to sample sizes being too small for analysis.

	Period				
	92-1	92-2	92-3	93-1	93-2
Long-tailed Tit	73.8	66.7	33.7	97.4	
Great Tit	77.7	30.0	31.5	69.4	39.5
Marsh Tit	51.0	24.7	46.6	60.7	28.3
Eastern Crowned Leaf Warbler	46.9	59.3	79.8	76.3	30.8
Japanese White-eye			93.0	100.5	
Narcissus Flycatcher	53.3	63.4	70.2	72.0	79.9
Brown Flycatcher				53.7	

creased in 1993.

In the first research periods of both years, the uses of tree species were similar among bird species and differed from the tree species composition in the study plot (Fig. 1). In the later research periods, bird species were divided into two groups: the first consisted of bird species that used trees in relation to the tree species composition of the area, while the second consisted of bird species that foraged in trees unrelated to their species composition (Fig. 1). Two *Parus* species usually belonged to the first group, while Narcissus Flycatcher and Japanese White-eye usually belonged to the second group. Long-tailed Tit and Eastern Crowned Leaf Warbler were classified into different groups in different research periods.

2) Foraging techniques on each tree species

Long-tailed Tit used all three foraging techniques with almost the same frequency (Table 3). Great Tit and Marsh Tit foraged by perch-gleaning most frequently but also hang-gleaned (30%). Eastern Crown Leaf Warbler foraged by hovering most frequently, but also perch-gleaned (30%). Japanese White-eye almost always foraged by perch-gleaning, and Narcissus Flycatcher and Brown Flycatcher almost always foraged by hovering. The variety of foraging techniques was maximal for the Long-tailed Tit, intermediate for the two *Parus* species, Eastern Crowned Leaf Warbler, and Japanese White-eye, and lowest for the two flycatcher species.

Foraging techniques used by each bird species were compared among tree species (Table 4). Significantly different frequencies of gleaning (perch-gleaning+hang-gleaning) and hovering among tree species were found in Long-tailed Tit (χ^2=6.20, df=2, P=0.045), Great Tit (χ^2=15.79, df=4, P=0.003) and Eastern Crowned Leaf Warbler (χ^2=16.92, df=4, P=0.002). Long-tailed Tit hovered more frequently on *B. platyphylla* than on *A. mono* (χ^2=6.24, df=1, P<0.05). Great Tit hovered more frequently on *B. platyphylla* than on *A. mono* and *Q. mongolica* (BP vs. AM: χ^2=11.13, df=1, P<0.001; BP vs. QM: χ^2=9.48, df=1, P<0.05). Eastern Crowned Leaf Warbler hovered more frequently on *B. platyphylla* than on *Q. mongolica* (χ^2=15.66, df=1, P<0.001). In all seven bird species, on the whole, hovering on *B. platyphylla* was more frequent than on *A. mono* or *Q. mongolica* (Mantel-Haenszel test with sequential Bonferroni method, BP vs. AM: χ^2=13.91, df=1, P<0.01; BP vs. QM χ^2=36.57, df=1, P<0.001).

Moreover, significantly different frequencies of perch- and hang-gleaning among tree species were found in Great Tit (χ^2=15.83, df=4, P=0.003) and Marsh Tit (χ^2=36.91, df=4, P<0.001). Both tits foraged by hanging more frequently on *A. mono* and *T. japonica* than on *Q. mongolica* (Great Tit: AM vs. QM: χ^2=8.61, df=1, P<0.05; QM vs. TJ: χ^2=8.98, df=1, P<0.05; Marsh Tit: AM vs. QM: χ^2=17.96, df=1, P<0.001; QM vs. TJ: χ^2=7.99, df=1, P<0.05). Marsh Tit also hang-gleaned more frequently on *T. japonica* than on *B. platyphylla* (χ^2=7.99, df=1, P<0.05). In the four gleaning species (Long-tailed Tit, *Parus* species, and Japanese White-eye), hang-gleaning on *A. mono* was more frequent than on *Q. mongolica* or *B. platyphylla* (Mantel-Haenszel test with sequential Bonferroni method, AM vs. QM: χ^2=16.02, df=1, P<0.001; AM vs. BP: χ^2=10.86, df=1, P<0.01), and hang-gleaning on *T. japonica* was more frequent than on *Q. mongolica*, *B. platyphylla* or *K. pictus* (TJ vs. QM: χ^2=31.75, df=1, P<0.001; TJ vs. BP: χ^2=14.00, df=1, P<0.01; TJ vs. KP: χ^2=8.07, df=1, P<0.05).

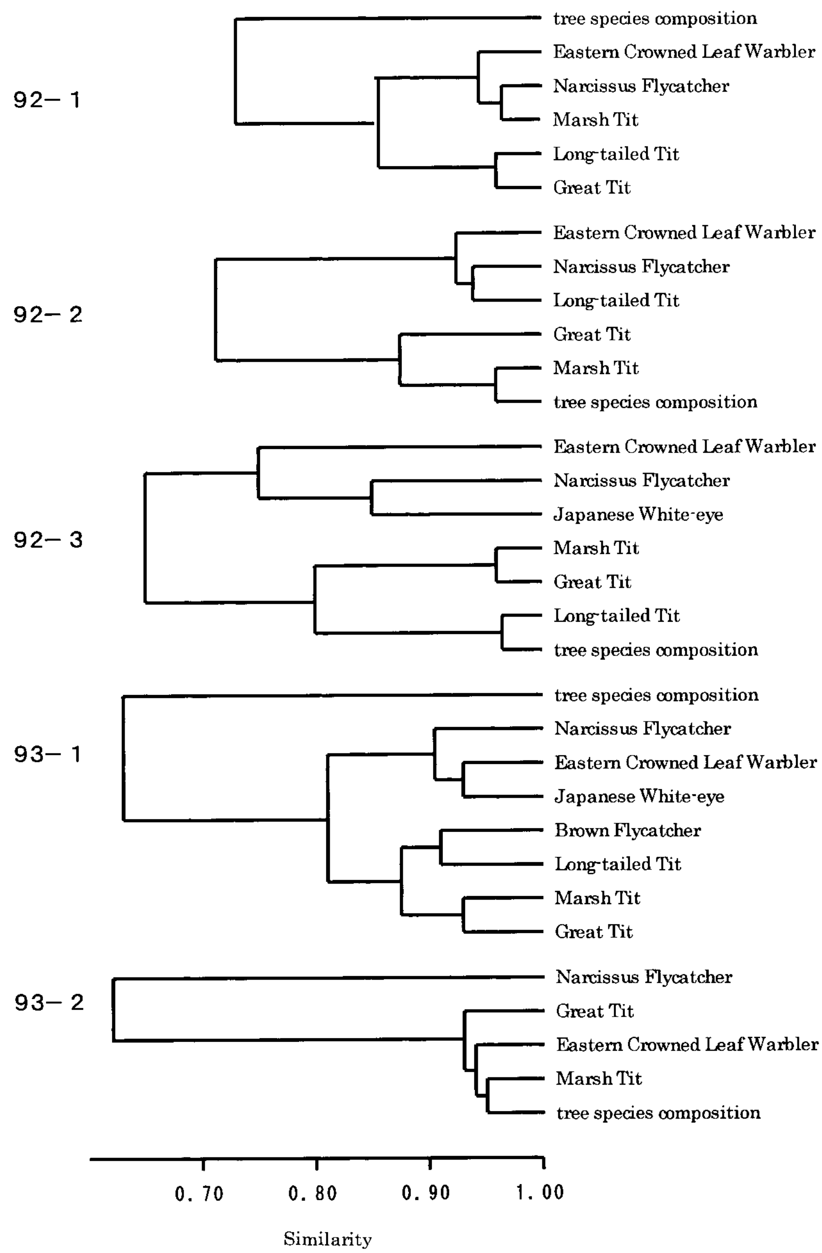

Fig. 1. Similarity between use of tree species by bird species and the tree species composition shown by means of α index (Pianka 1973). Dendrograms were constructed according to Mountford (1962).

These four bird species, Long-tailed tit, *Parus* species, and Eastern Crowned Leaf Warbler, which changed their foraging techniques between different tree species, used the widest range of foraging techniques (Table 3).

3) Prey abundances on each tree species

Arthropod abundances (dry mass/1 m^2 leaf surface area) changed seasonally, with the fluctuation patterns differing among tree species in each year (Fig. 2, two-way ANOVA, 1992: periods, $F_{83,2}$=4.78, P=0.011; tree species, $F_{83,3}$=1.64, P=0.19; periods×tree species, $F_{83,6}$=2.45, P=0.033; 1993: periods, $F_{113,1}$=8.86, P=0.004; tree species, $F_{113,5}$=8.02, P<0.0001; periods×tree species, $F_{113,5}$=1.13, P=0.35). Arthropod abundances differed among tree species in 92-1, 93-1, and 93-2 but not in 92-2, or 92-3 (one-way ANOVA; 92-1: $F_{27,3}$=5.26, P=0.006; 92-2: $F_{27,3}$=1.88, P=0.16; 92-3: $F_{27,3}$=0.62; P=0.61, 93-1: $F_{59,5}$=4.63, P=0.002; 93-2: $F_{53,5}$=4.51, P=0.002).

Table 3. Bird foraging techniques.

	Gleaning (%)		Hovering (%)	Diversity index Shannon's H′	Number of observation
	Perch-gleaning	Hang-gleaning			
Long-tailed Tit	25.7	45.5	28.8	1.54	132
Great Tit	60.0	32.3	7.7	1.25	637
Marsh Tit	59.7	33.3	7.0	1.24	1079
Eastern Crowned Leaf Warbler	28.5	4.7	66.8	1.11	240
Japanese White-eye	80.2	17.0	2.8	0.83	274
Narcissus Flycatcher	7.5	1.7	90.8	0.51	106
Brown Flycatcher	10.7	0.0	89.3	0.49	56

Table 4. Foraging techniques on each tree species. Parentheses show the number of observations. Because of small sample sizes comparison of Long-tailed Tit, Brown Flycatcher, and Japanese White-eye's foraging techniques on Caster arealia and Japanese linden were omitted (see Table 1 for AM, AH, QM, TJ, BP, and KP).

	Gleaning (%)	Hovering (%)		Gleaning		
				Perch-gleaning (%)	Hang-gleaning (%)	
Long-tailed Tit						
AM	83.7 (36)	16.3 (7)	*	37.2 (9)	62.8 (27)	
QM	70.6 (24)	28.4 (10)		58.8 (10)	41.2 (14)	
BP	56.0 (14)	44.0 (11)		68.0 (6)	32.0 (8)	
Great Tit						
AM	94.6 (194)	5.4 (11)	**	63.9 (120)	36.1 (74)	*
QM	94.7 (144)	5.3 (8)	*	78.3 (111)	21.7 (33)	*
TJ	86.5 (32)	13.5 (5)		54.0 (15)	46.0 (17)	
BP	82.8 (82)	17.2 (17)		75.8 (58)	24.2 (24)	
KP	92.3 (36)	7.7 (3)		64.1 (22)	35.9 (14)	
Marsh Tit						
AM	90.5 (134)	9.7 (14)		56.7 (70)	43.3 (64)	**
QM	95.8 (256)	4.2 (8)		78.4 (199)	21.6 (57)	**
TJ	78.4 (34)	21.6 (3)		45.9 (14)	54.1 (20)	**
BP	92.1 (232)	7.9 (20)		69.4 (155)	30.6 (77)	
KP	95.2 (80)	4.8 (4)		70.0 (55)	30.0 (25)	
Eastern Crowned Leaf Warbler						
AM	35.0 (7)	65.0 (13)		95.0 (6)	5.0 (1)	
QM	44.1 (49)	55.9 (62)	**	97.3 (46)	2.7 (3)	
TJ	25.0 (4)	75.0 (12)		100.0 (4)	0.0 (0)	
BP	5.7 (11)	84.3 (59)		95.7 (8)	4.3 (3)	
KP	23.1 (3)	76.9 (10)		92.3 (2)	7.7 (1)	
Japanese White-eye						
AM	96.0 (24)	4.0 (1)		76.0 (18)	24.0 (6)	
QM	100.0 (51)	0.0 (0)		90.2 (46)	9.8 (5)	
BP	66.7 (2)	33.3 (1)		100.0 (2)	0.0 (0)	
Narcissus Flycatcher						
AM	10.3 (3)	89.7 (26)		100.0 (3)	0.0 (0)	
QM	11.1 (9)	88.9 (72)		98.8 (8)	1.2 (0)	
TJ	6.7 (1)	93.3 (14)		100.0 (1)	0.0 (0)	
BP	4.6 (2)	95.4 (42)		100.0 (2)	0.0 (0)	
KP	5.7 (2)	94.3 (33)		97.3 (1)	2.7 (1)	
Brown Flycatche						
AM	15.4 (2)	84.6 (11)		100.0 (2)	0.0 (0)	
QM	19.1 (3)	80.9 (17)		100.0 (3)	0.0 (0)	
BP	0.0 (0)	100.0 (18)		100.0 (0)	0.0 (0)	

*: P<0.05, **: P<0.01.

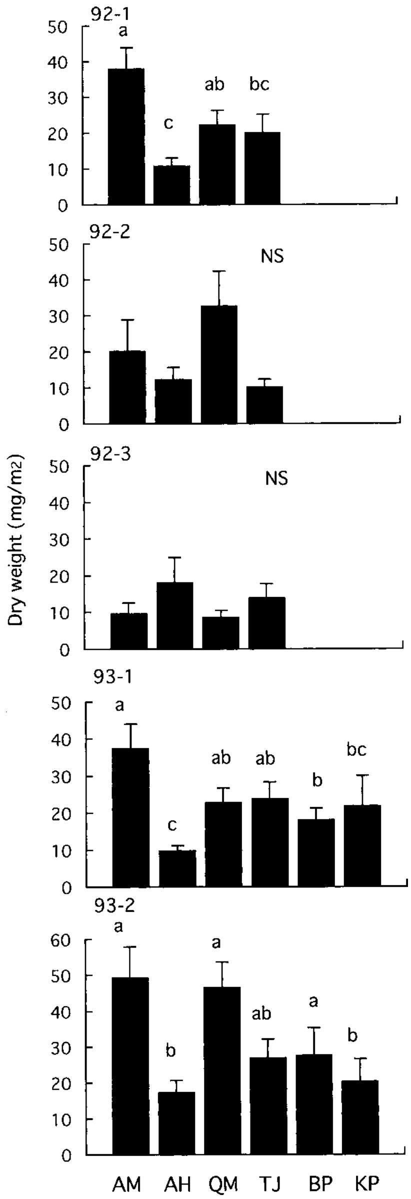

Fig. 2. Arthropod dry mass per 1 m^2 leaf area on various tree species (mean±SE). Refer to Table for AM, AH, QM, TJ, BP, and KP. BP and KP were not surveyed in 1992. Letters above vertical lines indicate the results of multiple comparison tests (Fisher's PLSD, $P<0.05$); the same letters indicate non-significant differences.

In the first research periods of each year, arthropod abundances were highest in *A. mono* (Fig. 2).

Of the 27 cases of correlation analyses for each bird species during each research period, there were seven positive relationships (26%) between selectivity by birds and arthropod abundance on different tree species (Table 5). Of the seven significant relationships, six (86%) were found for the four bird species, Long-tailed tit, *Parus* species, and Eastern Crowned Leaf Warbler, using wide range of foraging techniques (Table 3) and five (71%) were found during the first research periods.

DISCUSSION

Tree species supporting high prey abundance can be expected to be preferred by foraging birds (Hino et al. 2002). Prey abundance may explain why *A. mono* was most preferred by tit species during the first research periods each year. In most cases, however, tree species preferences were not related to prey abundances on trees. Some researchers have indicated that tree species preferences of birds are influenced not only by food abundance but also by food accessibility, that is foliage structure of trees and manoeverablity of birds both play a role (Holmes & Robinson 1981; Whelan 1989; Dias et al. 1998). For example, *Q. mongolica* was preferred but *B. platyphylla* was avoided by most bird species despite them supporting similar abundances of prey. This result may be attributable to the different accessibility of food in relation the foliage structure of these tree species. Almost all birds captured prey by hovering on *B. platyphylla* more frequently than on *Q. mongolica*. *B. platyphylla* has fine twigs, long petioles, and horizontally distributed leaves, which make searching and capturing prey while perching difficult, and make sallying or hanging from branches necessary. In contrast, *Q. mongolica*, which has thick twigs, very short petioles and a more three-dimensional distribution of leaves, provides more opportunities for foraging by perch-gleaning. Because perch-gleaning is a less energy-expensive foraging technique than hang-gleaning and hovering, capturing prey on *Q. mongolica* is less energy-expensive for birds than taking the same prey from *B. platyphylla*. Thus, birds should prefer *Q. mongolica* rather than *B. platyphylla*. Likewise, the food accessibility for gleaner species (Long tailed Tit, *Parus* species, and Japanese White-eye) may be influenced by the foliage structure of *A. mono* and *T. japonica*. These birds foraged frequently by hanging from twigs on these trees. Because leaves are distant from twigs, owing to the upward pointing long petioles of these trees, hang-gleaning would be an efficient technique to capture prey from the undersides of leaves where most caterpillars are found (Greenberg & Gradwohl 1980; Holmes & Schulz 1988).

The present results supported my hypothesis that there is a correlation between the variety of foraging

Table 5. Results of correlation analyses between Ivlev's electivity index of foraging bird species and arthropod abundances on each tree species. Spearman's rank correlation tests were one-tailed. Because of a few observations, results of Long-tailed Tit in 93-2, Japanese White-eye in 92-1, 92-2 and 93-2, and Brown Flycatcher in 92-1, 92-2, 92-3, and 93-2 were omitted.

	Periods (Number of tree species)				
	92-1 (4)	92-2 (4)	92-3 (4)	93-1 (6)	93-2 (6)
Long-tailed Tit	NS	NS	NS	(+)	
Great Tit	+	NS	NS	++	NS
Marsh Tit	NS	NS	NS	(+)	++
Eastern Crowned Leaf Warbler	NS	+	NS	NS	NS
Japanese White-eye			NS	NS	
Narcissus Flycatcher	NS	NS	NS	(+)	NS
Brown Flycatcher				NS	

Positive correlation: ++; $P<0.01$, +; $P<0.05$, (+); $0.1<P<0.05$.

techniques a bird uses and its flexibility of response to spatio-temporal changes in food resources. Bird species employing a wide range of foraging techniques, Long-tailed Tit, *Parus* species, and Eastern Crowned Leaf Warbler, changed their foraging techniques among different tree species. This must be an effective foraging tactic because the most efficient technique will depend on foliage structure. In contrast, birds with specialized foraging techniques did not show such a flexible response among tree species. The tree species that such specialists can forage from efficiently must be constrained by foliage structure. Japanese White-eye, a perch-gleaning specialist, would find it difficult to capture prey on trees with leaves distant from twigs, from which they cannot reach the leaves, or on trees with fine twigs where they cannot perch. Flycatchers, hovering specialists, are unlikely to be able to capture prey inhabiting rolled leaves because they cannot open such leaves or insert their bills into such leaves while holding branches or leaves (Murakami 1999).

The foraging techniques used were also related to a bird's response to seasonal changes in food resources. In the first research periods each year, birds resembled one another in their use of tree species, and their use differed considerably from the natural tree species composition. That is, all seven bird species were actively selecting the same particular tree species. In the later research periods, however, two different responses were found among bird species. Bird species with a wide range of foraging techniques (Long-tailed Tit and *Parus* species) changed and became non-selective, while those with specialized techniques (Japanese White-eye and flycatcher species) remained selective. In the late periods, Eastern Crowned Leaf Warbler was selective in 1992 but not selective in 1993. This yearly change may be attributable to this species' intermediate range of foraging techniques. Contrary to expectation, Long-tailed Tit, which has the widest range of foraging techniques, remained selective in 1992, although thus difficult to interpret result may have been because of the small sample size (N=21).

Why did birds using a wide range of foraging techniques become generalized in selecting tree species in later seasons? MacArthur (1972) predicted that foragers should be more specialized in productive than in unproductive environments. The same prediction was also given by the average-rate maximizing model combining the prey and patch models (Stephens & Krebs 1986). The present study showed that either prey abundance did not change, or it increased in later seasons. I expect, however, that a birds' requirement for prey is higher during the later research periods (early June to early July) owing to the addition of nestlings and fledglings. Accordingly, the non-selective use of tree species by bird species with a wide range of foraging techniques may have been an appropriate response to the seasonal change in prey abundance.

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