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Temporal changes in foraging niche among breeding tits (*Paridae*) in a Korean temperate deciduous forest

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The temporal change of foraging niche among breeding tits (Great Tit *Parus major*, Varied Tit *P. varius*, Marsh Tit *P. palustris* and Coal Tit *P. ater*) was studied in a Korean temperate deciduous forest from December 1998 to June 1999. We studied foraging niches in terms of foraging location, foraging maneuver and prey size, and measured morphological characters of tits. Great Tit had the largest body length among tits. There was significant difference in foraging locations among months and across species. Foraging maneuvers and prey sizes did not significantly differ among months, but showed inter-specific differences. There was a negative correlation between body weight and the use of the hanging maneuver among tits. This study suggests that closely related tits can coexist due to inter-specific differences in their foraging niche and because foraging locations change as the season advances.

1. Introduction

In temperate deciduous forest, tree leaves rapidly change in quality and quantity (Feeny 1970, Schultz *et al*. 1982, Schroeder 1986, Karban & Thaler 1999). Hence, it may be advantageous for canopy foraging birds to change their foraging heights (Murakami 1998, 2002) and tree species preference (Unno 2002) during the breeding season. However, many researchers have considered foraging maneuvers, foraging location, and prey sizes as static variables, and have pooled the data of foraging niche from a complete breeding period (Holmes *et al*. 1979, Holmes & Robinson 1981, Holmes & Schultz 1986, Hino *et al*. 2002). However, trees develop first a bud, then a soft leaf followed by a harder leaf (Kikuzawa 1983), which all may be different sources for insects that are preyed upon by birds in temperate deciduous forest. So, we hypothesize that the birds' foraging niche will be different across months and tree species during the spring period. Also, an eco-morphological approach suggests that there are differences in foraging maneuvers among phylogenetically and ecologically related species (Moreno & Carrascal 1993). In a Korean temperate deciduous forest, four closely related species of tits (Great Tit *Parus major*, Varied Tit *P. varius*, Marsh Tit *P. palustris* and Coal Tit *P. ater*) coexist and breed. Foraging niche shifts of mixed-species tits have been studied outside the breeding season (Jablonski and Lee 1998, 2002), but little research has been conducted on inter-specific difference of foraging niche and eco-morphological research among breeding tits. Therefore, we investigate temporal change in foraging niche among breeding tits in a Korean temperate deciduous forest.

2. Material and methods

2.1. Study area

This study was conducted at the Southern University Forests (SUF) of Seoul National University located in Kwangyang city of Chollanamdo province, Korea (35°01 N, 127°36 E) from March to June 1999. A 10-ha study plot (400 × 250m) was established. This plot consisted of temperate deciduous trees dominated by *Quercus serrata*, *Q. variabilis*, *Acer pseudosieboldianum*, *Lindera erythrocarpa*, *Carpinus laxiflora* and *Platycarya strobilacea*. The middle layer of the canopy was dominated by *Stewartia koreana*, *Meliosma myriantha*, *M. oldhamii*, *Ilex macropoda*, *Sapium japonicum*, *Styrax obassia*, *S. japonica* and *Symplocos chinensis* for. *pilosa*. The shrub layer was dominated by *Sasa borealis*, *Deutzia parviflora* and *Stephanandra incisa*. A more detailed description of the study area is given in Park (2001).

2.2. Bird foraging and morphological characters of tits

In the study area, the densities of *P. major*, *P. varius*, *P. palustris* and *P. ater* were estimated by territory mapping methods as 60, 60, 75 and 75 pairs per 100 ha, respectively (Park 2001). We captured tits from December 1998 to February 1999 by mist nets, and banded them with color ring to allow identification of individuals. Furthermore, we searched for nests of newcomers in the study area and banded breeding individuals. To avoid bias from repeated observations of the same individuals, we collected data while walking steadily within the study area. We walked along alternate, numbered lines in the long dimensions of the grid. Lines walked and the direction of travel was regularly selected to ensure an even visit of study area. We recorded the number of foraging behavior per thirty seconds (Altmann 1974). Each observation bout of an individual bird was planned to consist of 30–40 observations. We collected behavioral data using binoculars (8 × 30) between 07:00 and 12:00 from early April to late June in 1999. Each time a bird was observed attacking a prey item, we recorded the maneuver of the attack and the foraging location. Observations on the foraging of fledglings were excluded from the analysis.

A foraging bird was followed for as long as we could keep it in sight (Holmes & Schultz 1986). We differentiated foraging techniques into three types (sally-hovering, perch-gleaning, hang-gleaning; Remsen & Robinson 1990). Foraging locations were classified into air (AR), leaf (LF), twig (TG), bud (BD) and litter (LT). We recorded the length of larvae prey as either large (over 2cm), middle (over 1cm and below 2cm), or small (below 1cm), estimated using the beak length as a scale (Seki & Takano 1998). We measured total length, length of tail and tarsus, length of middle and hind toe, and wing length of tits captured by mist nets. We measured the length, width and depth of bill by digital calipers (Mitutoyo CD-50) to the nearest 0.01 mm. To eliminate size effects we divided lengths of wing, tail and toes by body length, and tarsus length was divided by cubic root of the body mass (Moreno & Carrascal 1993). Foraging rate was calculated as the number of prey captured per minute. The diversity of foraging niche was calculated by using the Shannon entropy: $H' = -p_i\log(p_i)$, in which p_i is the proportion of observations in each category (Shannon & Weaver 1949). Inter-specific differences of foraging niche and morphological characters were analyzed by the two-way ANOVA (with factors month and species). Monthly changes and inter-specific differences in the foraging location, maneuver and prey use were analyzed by a two-way MANOVA (with factors month and species) based on the frequencies of each item. Percentage data were arc-sin transformed to standardize variances. The data was used for non-metric multidimensional scaling performed on PAST version 1.32(Ø. Hammer, D.A.T. Harper and P.D. Ryan, University of Oslo, Norway), which was used for describing the seasonal changes in the multidimensional foraging niches of different tit species (Rytkönen

Table 1. Mean values of morphological characters of four species of tits used in this study.

Species	N	Total length (mm)	Weight (g)	Bill length (mm)	Bill width (mm)	Bill depth (mm)	Relative wing length	Relative tail length	Relative tarsus of middle toe^{1}	Relative length of hind toe^{1}	Relative length
Parus major	5	144.6^{a3}	16.60^{b}	14.92^{a}	7.00^{a}	5.46^{a}	0.99^{a}	0.88^{a}	7.31^{b}	0.09^{a}	0.11^{a}
Parus varius	5	136.2^{b}	18.32^{a}	15.90^{a}	6.06^{b}	5.24^{a}	0.94^{ab}	0.62^{c}	7.90^{a}	0.09^{a}	0.11^{a}
Parus palustris	5	123.6^{c}	11.38^{c}	9.98^{b}	5.34^{c}	4.56^{b}	0.85^{b}	0.71^{b}	7.36^{b}	0.08^{b}	0.09^{b}
Parus ater	5	112.2^{d}	8.54^{d}	8.46^{c}	4.72^{d}	4.02^{c}	0.82^{b}	0.63^{c}	7.51^{ab}	0.06^{c}	0.07^{c}

1 These values were calculated by dividing by body length (excluding tail length from total length).
2 The value was calculated by dividing by cubic root of body weight.
3 Characters show that duncan groups among four species.

& Krams 2003). All statistical tests were two tailed, and statistical significance was evaluated at $\alpha<0.05$.

3. Results

3.1. Morphological characters of tits

The species differed in size in all measured variables (Table 1: total length; $F_{3,16} = 51.51$, $P < 0.0001$, bill width; $F_{3,16} = 75.99$, $P < 0.0001$, bill length; $F_{3,16} = 48.32$, $P < 0.0001$, bill depth; $F_{3,16} = 46.37$, $P < 0.0001$, relative wing length; $F_{3,16} = 4.09$, $P < 0.05$, relative length of middle toe; $F_{3,16} = 20.90$, $P < 0.0001$, hind toe; $F_{3,16} = 26.76$, $P < 0.0001$, weight; $F_{3,16} = 68.19$, $P < 0.0001$, relative tarsus length; $F_{3,16} = 4.10$, $P < 0.05$). In general, the size order from largest to smallest was Great Tit (*P. major*), Varied Tit (*P. varius*), Marsh Tit (*P. palustris*) and Coal Tit (*P. ater*) (see Table 1 for mean sizes).

3.2. Foraging location

MANOVA analysis revealed that foraging location differed among bird species (Hotelling-Lawley Trace: bird species, value = 5.82, F = 11.63, df = 12, $P < 0.0001$) and across seasonal period (value = 11.31, F = 33.94, df = 8, $P < 0.0001$) with significant interaction (F = 37.48, df = 59, $P < 0.0001$). Tits utilized more air and leaf locations in May and June than in April. Tits located more prey in buds in April than in May and June, and they used the litter more in April and June than in May.

Table 2. Monthly usage (expressed in percentage of the total number of observations) and niche width of foraging locations used by four species of tits during three months in spring. Species names are abbreviated. PM: *Parus major*, PV: *P. varius*, PP: *P. palustris*, PA: *P. ater*.

	April				May				June			
Locations	PM^{a}	PV	PP	PA	PM	PV	PP	PA	PM	PV	PP	PA
Air (AR)	2.8	7.3	6.2	3.8	8.5	20.8	13.7	7.1	9.8	13.6	13.8	9.8
Leaf (LF)	20.8	28.7	36.9	49.0	59.6	72.9	77.4	83.3	53.7	70.5	75.5	90.2
Twig (TG)	37.5	7.3	7.8	11.3	31.9	4.2	8.9	9.5	36.6	2.3	10.6	0.0
Bud (BD)	15.3	36.7	42.3	34.0	0.0	2.1	0.0	0.0	0.0	2.3	0.0	0.0
Litter (LT)	23.6	20.0	6.8	1.9	0.0	0.0	0.0	0.0	0.0	11.4	0.0	0.0
No. of observations	72	150	309	159	47	48	168	126	41	44	188	102
Niche width (H')	1.42	1.43	1.29	1.16	0.88	0.77	0.69	0.56	0.93	0.94	0.72	0.32

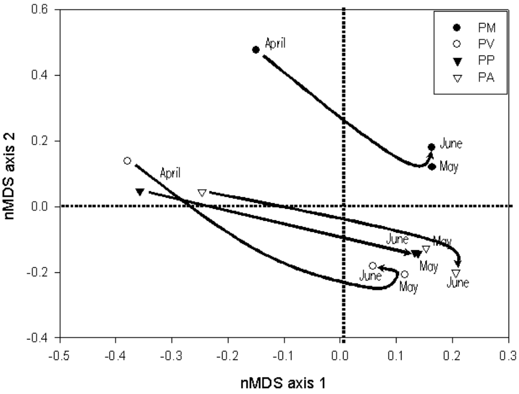

Fig. 1. The similarity of foraging niches Great Tit (PM), Varied Tit (PV), Marsh Tit (PP), and Coal Tit (PA) during the breeding season as described by using non-metric multidimensional scaling (NMDS, using PAST 1.32). The foraging niche (5 locations × 3 months) of the four species was analyzed.

Of all the four tit species, *P. major* used twigs as foraging location in each month. Niche width of foraging location was significantly ($F_{5,6}$ = 25.06, P < 0.05) different among species (F = 9.86, df = 3, P = 0.0098) and months (F = 47.87, df = 2, P = 0.0002). Value of niche width in April (1.33 ± 0.09, n = 4) was higher than in May (0.73 ± 0.29, n = 4) and in June (0.73 ± 0.13, n = 4), and the value of niche width of *P. ater* was lower than of *P. major*, *P. varius* and *P. palustris* (Table 2). The foraging niches of location were described by using non-metric multidimensional scaling (NMDS, Fig. 1). The stress for the 2-dimensional result was 6.65%, i.e. the points in the space matched the given similarities well. The foraging locations approach the same directions toward June (Fig. 1). However, foraging niche of Great Tits differed markedly from other tits.

3.3. Foraging maneuver

MANOVA analysis revealed that foraging maneuver differed among bird species (summary data in Table 3; Hotelling-Lawley Trace: bird species, value = 9.66, F = 19.32, df = 6, P < 0.0001), but did not differ across seasons (value = 0.13, F = 0.40, df = 4, P < 0.81) with significant interaction (F = 22.64, df = 35, P < 0.0001). Perch-gleaning (PG, Table 3) was the most common foraging maneuver utilized ($F_{3,8}$ = 17.20, P < 0.001). This maneuver was most frequently used by *P. major* (84.9 ± 6.5%, n = 3), followed by *P. varius* (71.4 ± 8.8%, n = 3), *P. palustris* (60.5 ± 4.3%, n = 3) and *P. ater* (46.7 ± 3.4%, n = 3). However, hang-gleaning (HG; Table 3) was most frequently utilized by *P. ater* (46.3 ± 1.8%, n = 3), followed by *P. palustris* (25.2 ± 2.6%, n = 3), *P. varius* (12.9 ± 2.8%, n = 3) and *P. major* (4.1 ± 3.7%, n = 3).

Tits showed no significant difference in niche width of foraging maneuvers among months, but did show significant inter-specific differences (F = 5.46, P < 0.05). *P. major* showed the narrowest niche width among tits (Table 3, 0.48 ± 0.16, n = 3) in terms of foraging maneuvers over the three months compared to *P. palustris* (0.89 ± 0.08, n = 3), *P. ater* (0.89 ± 0.18, n = 3) and *P. varius* (0.78 ± 0.13, n = 3).

The foraging niches of maneuver were described by using non-metric multidimensional

Table 3. Monthly usage (expressed in percentage of the total number of observations) and niche width of different foraging maneuvers employed by four species of tits. Species names are abbreviated. PM: *Parus major*, PV: *P. varius*, PP: *P. palustris*, PA: *P. ater*.

Maneuvers	April				May				June			
	PM	PV	PP	PA	PM	PV	PP	PA	PM	PV	PP	PA
Sally-hovering (SH)	14.5	9.2	6.6	3.8	8.9	22.7	15.0	7.1	9.8	15.4	15.2	9.8
Perch-gleaning (PG)	78.2	78.3	66.7	50.6	91.1	61.4	58.2	44.4	85.4	74.4	62.6	45.1
Hang-gleaning (HG)	7.3	12.5	26.7	45.5	0.0	15.9	26.8	48.4	4.9	10.3	22.2	45.1
No. of observations	55	120	288	156	45	44	153	126	41	39	171	102
Niche width (H')	0.66	0.67	0.80	0.83	0.30	0.93	0.95	0.90	0.51	0.74	0.91	0.95

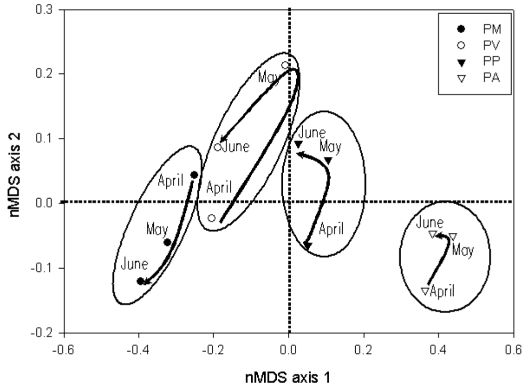

Fig. 2. The similarity of foraging niches Great Tit (PM), Varied Tit (PV), Marsh Tit (PP), and Coal Tit (PA) during the breeding season as described by using non-metric multidimensional scaling (NMDS, using PAST 1.32). The foraging niche (3 maneuvers × 3 months) of the four species was analyzed.

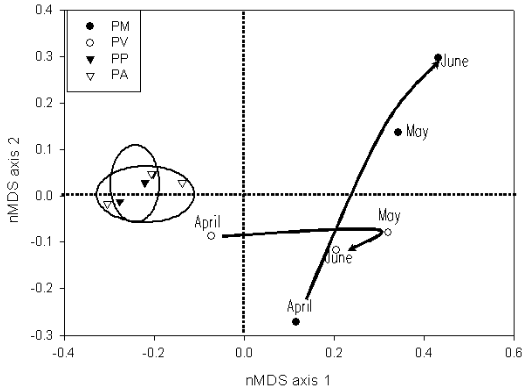

Fig. 3. The similarity of foraging niches Great Tit (PM), Varied Tit (PV), Marsh Tit (PP), and Coal Tit (PA) during the breeding season as described by using non-metric multidimensional scaling (NMDS, using PAST 1.32). The foraging niche (3 prey size × 3 months) of the four species was analyzed.

scaling (NMDS) (Fig. 2). The stress for the 2-dimensional result was 2.75%. The foraging maneuvers of tits divide each other in each month. Also, direction of foraging behavior of Great Tit was different compared to the three other tits (Fig. 2).

3.4. Prey size

MANOVA analysis revealed that prey sizes differed among the four tit species (Hotelling-Lawley Trace: species, value = 5.25, F = 10.50, df = 6, P = 0.0003) with significant interaction (F = 5.82, df = 35, P = 0.0014). Comparing the prey size used by tits among species and months, prey below one-centimeter size was significantly more frequently ($F_{3,8}$ = 14.57, P < 0.005) utilized by *P. palustris* (81.3 ± 4.6, n = 3) and *P. ater* (79.7 ± 7.9, n = 3) than by *P. varius* (42.2 ± 20.8, n = 3) and *P. major* (23.2 ± 14.7, n=3). Prey over one-centimeter and below two-centimeter size was significantly ($F_{3,8}$ = 5.12, P < 0.05) more often utilized by *P. varius* (42.6 ± 7.0, n = 3) and *P. major* (39.0 ± 19.5, n = 3) than by *P. ater* (16.5 ± 4.9, n = 3) and *P. palustris* (14.9 ± 1.2, n = 3). Prey over two-centimeter size was mostly ($F_{3,4}$ = 17.93, P < 0.01) used by *P. major* (56.7 ± 13.0, n = 2), followed by *P. varius* (22.7 ± 0.5, n = 2), *P. palustris* (5.8 ± 0.8, n = 2) and *P. ater* (5.7 ± 0.3, n = 2) (Table 4). The foraging niches of prey size were described by using non-metric mul-

Table 4. Monthly usage (expressed as a percentage of the total number of observations) and niche width of differently sized prey caught by four species of tits. Species names are abbreviated. PM: *Parus major*, PV: *P. varius*, PP: *P. palustris*, PA: *P. ater*.

Prey size	April				May				June			
	PM[a]	PV	PP	PA	PM	PV	PP	PA	PM	PV	PP	PA
<1cm	38.9	65.3	86.4	88.1	21.0	25.0	79.8	78.6	9.7	36.4	77.6	72.5
1–2cm	61.1	34.7	13.6	11.9	31.6	47.7	15.0	15.9	24.4	45.5	16.0	21.6
>2cm	0.0	0.0	0.0	0.0	47.4	27.3	5.2	5.5	65.9	18.1	6.4	5.9
No. of observations	72	150	309	159	47	48	165	126	41	44	188	102
Niche width (H')	0.67	0.65	0.40	0.36	1.05	1.05	0.62	0.64	0.85	1.04	0.67	0.73

tidimensional scaling (NMDS) (Fig. 3, stress for the 2-dimensional result was 1.75%). The foraging niche of Great Tits showed a different direction compared to that of the Varied Tit. Marsh Tits and Coal Tits divided the foraging niche of prey size with Great Tits and Varied Tits.

3.5. Relationship between hanging ratio and relative tarsus length

Percent of hanging was not correlated with relative tarsus length among the four tit species ($r = -0.04$, $P < 0.9607$, $n = 4$), although it significantly correlated with the relative tarsus length ($r = 1.0$, $P < 0.0001$, $n = 3$) after excluding *P. varius*. Furthermore, percentage of hanging was negatively correlated with the logarithm of body weight ($r = -0.80$, $P < 0.0200$, $n = 4$). Foraging rate was significantly ($F_{3,338} = 15.46$, $P < 0.0001$) higher in *P. ater* (2.91 ± 1.1, n = 44) than in *P. palustris* (2.53 ± 1.3, n = 145), *P. varius* (2.18 ± 1.0, n = 98) and *P. major* (1.58 ± 0.6, n = 55).

4. Discussion

4.1. Temporal changes in foraging niches

We analyzed the temporal changes in foraging niche in terms of locations, maneuvers and prey sizes in four tit species that co-occur in a temperate forest. Tits showed temporal changes in the foraging locations of leaf, twig, bud, and litter, respectively. They did not show significant temporal changes of foraging maneuvers and prey sizes. In April, tits mostly utilize buds and litter, and then change foraging location to leaf and air after May. Furthermore, tits utilize the litter in June. This indicates that foraging locations of tits are temporally flexible, because the use of air and leaf for foraging increases, whereas the use of buds decreased as trees develop their leaves. However, preference for foraging in the litter is high in April and June.

In terms of foraging locations, tits frequently utilize leafs in each month. Twigs (which form the inner space of a tree) are more used by the largest tit, *P. major*, compared to the others species. The same result has been found in a Japanese deciduous forest (Haneda and Nakamura 1967, Nakamura 1978) and in European coniferous forest (Hogstad 1978, Alatalo 1981, Alatalo *et al*. 1986, Alatalo *et al*. 1987, Alatalo and Moreno 1987). Two explanations can supported the high use of twigs as foraging locations for *P. major*. First, larger birds can more freely move at microhabitat space surrounded by spare twigs than in dense leafy microhabitat. Second, *P. major* can more easily utilize perch-gleaning maneuvers on twigs than on leafs. So, leaf arrangement of trees (Whelan 2001) and morphological traits of *P. major* can affect its high use of twigs.

4.2. Inter-specific difference of foraging niches

Tits show no temporal change, but they do show inter-specific differences in terms of foraging maneuvers and prey sizes. *P. major* shows a different direction of foraging maneuvers compared to other tits and they show segregate distribution of monthly changes of foraging maneuvers (Fig. 2). Tits typically use the maneuver of perch gleaning (PG) which is the least costly maneuver to pick food items from substrate (Remsen and Robinson 1990). *P. major* preferred the perch-gleaning maneuver. Previous work has shown that hanging ratio relates to relative tarsus length among inter-specific competition (Moreno and Carrascal 1993, Carrascal *et al.* 1995), and to correlate with body weights among intra-specific competition (Barbosa *et al*. 2000). However, our results show a significant correlation between body weight and percentage of hanging among species (Fig. 1). But after excluding *P. varius*, percentage of hanging was correlated with relative body length. *P. varius* utilizes frequently the hanging behavior, although it has the highest value of relative tarsus length and body weight among tits. This result might be related with the inter-specific competition between *P. major* and *P. varius*, because these two species share similar morphological characters (Table 1). Furthermore, *P. major* preys more often on insect larvae over two centimeters than other species do. Nevertheless, *P. major* and *P. varius* did not show a significant difference for insect prey below two centimeters. Importantly, *P. major* and *P. varius* show different directions of foraging niche in dimension of prey size (Fig. 3). So, it can be suggested that *P. varius* more frequently uses smaller prey for maintaining the energy demand for heaviest body weight than *P. majo*r. And, it can be supported by that *P. varius* showed the higher value of foraging rate than *P. major*. Differences in prey-size preference has been found between single-prey loader *P. major* and multiple-prey loader *P. varius* (Mizutani & Hijii 2002). Our results suggest that closely related tits show inter-specific difference in foraging maneuver and prey size; *P. major* utilizes a relatively inflexible foraging maneuvering, and preys on prey over two-centimeter, but the others, including the large bodied *P. varius*, used more agile foraging maneuvers (Morse 1978, Perrins 1979, Hino *et al.* 2002) and diverse use of prey size.

4.3. Conclusions

Our results suggest that closely related tits showed inter-specific difference of foraging location, foraging maneuver and use of prey size, and displayed a temporal change in foraging location during the spring period. Hence, when data on foraging niche is analyzed, data of foraging maneuver and use of prey size may be pooled, however data on foraging location needs to be considered in temporal scale. Furthermore, diverse trees that show different development stages (e.g. bud, soft leaf, and hard leaf) can help maintain diverse tits in a Korean temperate deciduous forest. Moreover, litter layer can be a food resource in April and June, so protection of litter layer can provide the diverse foraging location for tits. Furthermore, there should be further research on the inter-specific difference of social dominance, ecomorphology and foraging niche of tits in East Asia.

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Lisääntyvien tiaisten (Paridae) ruokailupaikkojen ajalliset muutokset Korean lauhkeassa lehtimetsässä.

Lisääntyvien tiaisten (talitiainen *Parus major*, kirjotiainen *P. varius*, viitatiainen *P. palustris*, kuusitiainen *P. ater*) ruokailutapojen ajallista vaihtelua tutkittiin Korean lauhkean vyöhykkeen lehtipuumetsissä joulukuusta 1998 kesäkuuhun 1999. Tutkimme ruokailupaikkoja, tiaisten liikkumista ruokailun yhteydessä, saaliin kokoja, sekä mittasimme tiaisten morfologiset ominaisuudet. Talitiaisen ruumiinpituus oli tiaisista suurin. Ruokailupaikat erosivat toisistaan merkittävästi kuukausien ja lajien välillä. Liikkuminen ja saaliin koko erosivat toisistaan merkitsevästi lajien välillä, mutta ajallista vaihtelua näissä ominaisuuksissa ei ollut. Ruumiin koko oli käänteisesti verrannollinen roikkumisen määrään ruokailtaessa. Tämä viittaa siihen, että toisilleen läheistä sukua olevat tiaiset pystyvät jakamaan saman ympäristön, koska niiden ruokailukäyttäytymisessä on lajienvälisiä eroja ja koska ruokailupaikat vaihtuvat lisääntymiskauden edetessä.

References

Alatalo, R.V. & Moreno, J. 1987: Body size, interspecific interactions, and use of foraging sites in Tits (Paridae). — Ecology 68: 1773–1777.

Alatalo, R.V. 1980: Seasonal dynamics of resource partitioning among foliage-gleaning passerines in Nothern Finland. — Oecologia 45: 190–196.

Alatalo, R.V. 1981: Interspecific competition in tits Parus spp. and the goldcrest *Regulus regulus*: foraging shifts in multispecies flocks. — Oikos 37: 335–344.

Alatalo, R.V. 1982: Multidimensional foraging niche organization of foliage-gleaning birds in northern Finland. — Ornis Scandinavica 13: 56–71.

Alatalo, R.V., Eriksson, D., Gustafsson, L. & Larsson K. 1987: Exploitation competition influences the use foraging sites by tits: experimental evidence. — Ecology 68: 284–290.

Alatalo, R.V., Gustafsson, L. & Lundberg, A. 1986: Interspecific competition and niche shifts in tits (Parus spp.): an evaluation of non-experimental data. — American Naturalist 127: 819–834.

Altmann, J. 1974: Observation study of behavior: sampling methods. — Behaviour 49: 227–265.

Austin, G.T. 1970: Breeding birds of desert riparian habitat in southern Nevada. — Condor 72: 431–436.

Barbosa, A., Barluenga, M. & Moreno, E. 2000: Effects of body mass on the foraging behaviour of subordinate Coal Tits Parus ater. — Ibis 142: 428–434.

Carrascal, L.M., Moreno, E. and Mozetich, I.M. 1995: Ecological plasticity of morphological design: an experimental analysis with tit species. — Canadian Journal of Zoology 73: 2005–2009.

Feeny, P. 1970: Seasonal changes in oak leaf tannin and nutrients as a cause of spring feeding by winter moth caterpillars. — Ecology 51: 565–581.

Haneda, K & Nakamura, T. 1967: Ecological study of the bird community in Otanomous Plateau, Shiga. Bulletin of Nature Education in Shiga Heights. — Shinshu University 6: 1108–1124. (Japanese with English abstract)

Hino, T., Unno, A. & Nakano, S. 2002: Prey distribution and foraging preference for tits. — Ornithological Science 1: 81–87.

Hogstad, O. 1978: Differentiation of foraging niche among tits Parus spp. in Norway during winter. — Ibis 120: 139–146.

Holmes, R.T. & Robinson, S.K. 1981: Tree species preference of foraging insectivorous birds in a Northern hardwoods forest. — Oecologia 48: 31–35.

Holmes, R.T. & Schultz, J.C. 1986: Food availability for forest birds: effect of prey distribution and abundance on bird foraging. — Canadian Journal of Zoology 66: 720–728.

Holmes, R.T., Bonney, R.E.Jr. & Pacala S.W. 1979: Guild structure of the Hubbard Brook bird community: a multivariate approach. — Ecology 60: 512–520.

Jablonski, P.G. & Lee S.D. 1998: Foraging niche differences between species are correlated with body-size differences in mixed-species flocks near Seoul, Korea. — Ornis Fennica 76: 17–23.

Jablonski, P.G. & Lee S.D. 2002: Foraging niche shifts in mixed-species flocks of tits in Korea. — Journal of Field Ornithology 73: 246–252.

Karban, R. & Thaler, J.S. 1999: Plant phase change and resistance to herbivory. — Ecology 80: 510–517.

Kikuzawa K. 1983: Leaf survival of woody plants in deciduous broad-leaved forests. 1. tall trees. — Canadian Journal of Botany 61: 2133–2139.

Levins, R. 1968: Evolution in changing environments. — Princeton Univ. Pres, Princeton.

Mizutani, M. & Hijii, N. 2002: The effects of arthropod abundance and size on the nestling diet of two Parus species. — Ornithological Science 1: 71–80.

Moreno, E. & Carrascal, L.M. 1993: Leg morphology and feeding postures in four Parus species: an experimental ecomorphological approach. — Ecology 74: 2037–2044.

Morse, D.H. 1974: Niche breadth as a function of social dominance. — American Naturalist 108: 818–830.

Morse, D.H. 1978: Structure and foraging patterns of flocks of tits and associated species in an English woodland during the winter. — Ibis 120: 298–312.

Murakami, M. & Wada, N. 1997: Difference in leaf quality between canopy trees and seedlings affects migrations and survival of spring-feeding moth larvae. — Canadian Journal of Forest Research 27: 1351–1356. (In Japanese with English abstract)

Murakami, M. 1998: Foraging habitat shift in the narcissus flycatcher, Ficedula narcissina, due to the response of herbivorous insects to the strengthening defenses of canopy trees. — Ecological Research 13: 73–82.

Murakami, M. 2002: Foraging mode shifts of four insectivorous bird species under temporally varying resource distribution in a Japanese deciduous forest. — Ornithological Science 1: 63–69.

Nakamura, T. 1978: A study of Paridae community in Japan. Ecological segregation of species by the differences of use of bill in space and technique. — Journal of the Yamashina Institute for Ornithology 10: 94–118. (In Japanese with English abstract)

Park, C.R. 2001: Interaction Networks among Tits, Insects and Plants during the Breeding Season. Ph.D. dissertation, Department of Forest Resources, Graduate School of Seoul National University, Seoul, Korea.

Perrins, C.M. 1979: British tits. — Collins, London (New Naturalist Series).

Remsen, J.V. Jr. & Robinson, S.K. 1990: A classification scheme for foraging behavior of birds in terrestrial habitats. — In Avian Foraging: theory, morphology, and applications (eds. Morrison, M.L., Ralph, C.J., Verner, J. & Jehl J.R. Jr.): 144–160. Allen Press, Lawrence, Kansas, USA.

Rytkonen S. & Krams I. 2003: Does foraging behaviour explain the poor breeding success of Great Tits Parus major in northern Europe? — Journal of Avian Biology 34: 288–297.

Schroeder, L.A. 1986: Changes in tree leaf quality and growth performance of Lepidopteran larvae. — Ecology 67: 1628–1636.

Schultz, J.C., Nothangle, P.J. & Baldwin, I.T. 1982: Seasonal and individual variation in leaf quality of two northern hardwoods tree species. — American Journal of Botany 69: 753–759.

Seki, S. & Takano, H. 1998: Caterpillar abundance in the territory affects the breeding performance of Great Tit Parus major minor. — Oecologia 114: 514–521.

Shannon, C.E. & Weaver, W. 1949: The mathematical theory of communication. — University of Illinois press.

Unno, A. 2002: Tree species preference of insectivorous birds in a Japanese deciduous forest: the effect of different foraging techniques and seasonal change of food resources. — Ornithological Sciences 1: 133–142.

Whelan, C.J. 2001: Foliage structure influences foraging of insectivorous forest birds: an experimental study. — Ecology 82: 219–231.