

The effects of arthropod abundance and size on the nestling diet of two *Parus* species

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Abstract Feeding habits of *Parus major* and *P. varius* inhabiting coniferous plantations of *Cryptomeria japonica* and *Larix kaempferi*, each containing a small area of deciduous broad-leaved trees, were analyzed in relation to the abundance and size distribution of arthropods. In a *C. japonica*-dominated (*CJ*) area, *C. japonica* trees were mainly used by *P. major* only, while deciduous broad-leaved trees were used by both *Parus* species. In a *L. kaempferi*-dominated (*LK*) area, both *Parus* species used *L. kaempferi* trees and deciduous broad-leaved trees. The composition of nestling diets differed between *Parus* species. For prey size, the difference in the breadth was smaller and the overlap was larger between areas than between species. These results suggest that each *Parus* species preferred a specific size class of prey. That is, the single-prey loader *P. major* preferred large prey, whereas the multiple-prey loader *P. varius* preferred small prey. The abundance and size distribution of arthropods greatly differed among foraging microhabitats. Both *Parus* species selectively used foraging microhabitats according to their prey-size preference.

Key words Diet selection, Foraging microhabitat, Nestling diet, *Parus major*, *Parus varius*, Size preference

Forest-dwelling insectivorous birds, including Paridae, depend on arthropods for food, especially during the breeding season. The structure, biomass and dynamics of arboreal arthropod communities may vary depending on the tree species composition and structural features of forests (e.g. Stork et al. 1997), thus the characteristics and availability of arthropods as a food resource for insectivorous birds may differ among different forest types. In general, *Parus* species depend on caterpillars, mostly lepidopteran and hymenopteran larvae, for primary food resources (Perrins 1979), but their food composition differs among forest types (Gibb & Betts 1963; van Balen 1973). Although many studies have focused on the effects of differences in the availability of caterpillars on the feeding habits or breeding ecology of *Parus* species (e.g. van Balen 1973; Yui 1988; Perrins 1991; van Noordwijk et al. 1995; Seki & Takano 1998), little attention has been paid to other arthropods, or to the whole arthropod community, as potential food resources.

According to the optimal-foraging theory, predators choose their diet to maximize their net rate of energy intake (cf. Krebs & Kacelnik 1991). Thus, the characteristics of arthropods, such as abundance, biomass and other specific features associated with their susceptibility to capture, are relevant to the profitability of each prey item and thus to the foraging decision by birds (Royama 1970; Hespenheide 1975). Also, it has been known for some time that birds differ interspecifically in their prey-size preferences, presumably associated with their morphological traits (e.g. Betts 1955; Gibb & Betts 1963; Diamond 1973; Eguchi 1979; Quinney & Ankney 1985; Török 1986; Díaz 1994).

In this paper, we describe the feeding habits of *Parus major* and *P. varius* in two coniferous plantations of the evergreen *Cryptomeria japonica* D. Don and the deciduous *Larix kaempferi* Carrière. Marked differences in the abundance, biomass, and composition of the arthropod community has previously been revealed between these two plantations (Hijii et al. 2001; Mizutani & Hijii 2001).

We demonstrate the effects of the abundance and size distribution of arthropods on microhabitat selec-

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tion by *Parus* species through their prey-size preference for their nestlings.

MATERIALS AND METHODS

1) Study site

The study was carried out in the Nagoya University Forest at Inabu, Aichi Prefecture, central Japan (980–1230 m a.s.l.; 35°11'N, 137°33'E). The annual air temperature averaged 8.3°C and the mean annual precipitation was 2250 mm (1981–1998). About 90% of the area of this experimental forest is dominated by plantations of *C. japonica*, *L. kaempferi* and *Chamaecyparis obtusa* Sieb. et Zucc. Small stands of deciduous broad-leaved trees such as *Quercus crispula*, *Carpinus tschonoskii*, *Prunus grayana* and *Acer sieboldianum* occur patchily, for the most part along ridges and streams. The height of dominant trees was 20–25 m and the age of the plantations was 21–40 years. The canopies of the plantations were closed; their understories were not dense and were heterogeneous, consisting mainly of *Lindera praecox* and *L. triloba*. For the purposes of this study, understory was defined as the ground flora rising no more than two metres above the ground.

Two adjoining study areas were established in the experimental forest: a *C. japonica*-dominated (*CJ*) area and a *L. kaempferi*-dominated (*LK*) area (Fig. 1). More than 50% of each area was covered with a plantation of each dominant conifer, while about 10% of each area consisted of deciduous broad-leaved trees. The remainder of each area consisted mainly of *Chamaecyparis obtusa* plantations and bare areas, both of which were rarely used by either *Parus* species. Censuses were conducted during the nestling period of early broods of the two *Parus* species in 1999.

2) Foraging microhabitat

From 23 May to 9 June 1999, the microhabitat use of foraging *Parus* species was surveyed using a line-census method. In each study area, two transects, each 50-m wide and 3.8-km long, covering 40% of the area, were surveyed six times. Whenever a bird was observed to forage on a prey item, its height above the ground, and the plant species from which it foraged, were recorded. Foraging microhabitat selection for tree layers was analyzed using the selectivity index defined as the ratio of percentage microhabitat use to percentage cover area for each tree species (Manly et al. 1993). The selectivity index is 0 when

the resource is not used at all, 1 when the resource is used as expected by chance, and larger than 1 when the resource is used selectively.

3) Nestling diet

From 14 May to 16 June 1999, nestling diet was recorded with an 8-mm video camera at six clutches of *P. major* (3 at *CJ* area and 3 at *LK* area) and five clutches of *P. varius* (3 at *CJ* area and 2 at *LK* area) in nest boxes. For each observation, two trials, each of six hours, were made in the first half (5–9 days of age) and the latter half (11–15 days of age) of the nestling period. We converted the recorded video movie into a computer file in non-compressed video format, then extracted several still images for each nest-visit. From the still images, prey items (at the order level or as “caterpillars”), and prey-size (body length) were recorded. Totals of 1181 feeding records were obtained on video for *P. major* and 406 for *P. varius*. Among them, clear pictures suitable for prey identification and for prey-size determination amounted to 1124 for *P. major* and 330 for *P. varius*. Dry weights (*W*, mg) of prey items were estimated from body lengths (*L*, mm) and regression equations made based on field samples (caterpillars and orthopteran insects) collected randomly in the study site

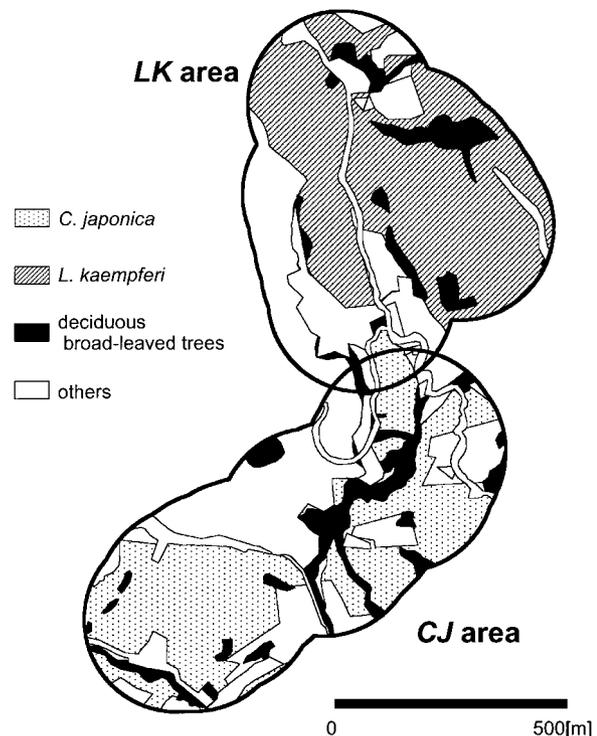


Fig. 1. The vegetation of the two study areas.

during the nestling period of early broods of two *Parus* species or from the literature.

For caterpillars the dry weight estimate was:

$$W=0.0011L^{3.00} \quad (n=103, r^2=0.91, P<0.001) \quad (1)$$

for orthopteran insects it was

$$W=0.0120L^{2.36} \quad (n=88, r^2=0.94, P<0.001) \quad (2)$$

and for other arthropods

$$W=0.0305L^{2.62} \quad (r^2=0.94: \text{Rogers et al. 1976}). \quad (3)$$

Prey size was defined as the dry mass (estimated as above) and classified according to size classes between 10^{-1} and $10^{2.5}$ mg dry weight (d.wt) at intervals of the power index 0.25. The breadth of the size-class distribution for prey items was evaluated using the Shannon-Wiener formula (Shannon & Weaver 1949),

$$H' = - \sum_j p_j \log p_j \quad (4)$$

where p_j is the proportion of prey individuals belonging to size class j . The degree of overlap between size-class distributions was evaluated using the multiplicative measures of niche overlap (Pianka 1973),

$$\alpha_{hi} = \frac{\sum_j p_{hj} p_{ij}}{\sqrt{\sum_j (p_{hj})^2 \sum_j (p_{ij})^2}} \quad (5)$$

where p_{hj} and p_{ij} are the proportions of prey individuals of the j th size class used by the h th and the i th species, respectively. The index α varies from 0, when size-class distributions are completely distinct, to 1, when they fully overlap.

4) Arthropod sampling

Arthropod sampling was conducted twice, on 18 May and 10 June 1999. Arthropods were collected from four foraging microhabitats: tree layers of *C. japonica*, *L. kaempferi* and deciduous broad-leaved stands using the branch clipping method, and from the understory using the beating method. Details of the protocol for the branch clipping method are described by Hijii et al. (2001). Arthropod sampling from *C. japonica* and deciduous broad-leaved stands was made in the *CJ* area, and that from a *L. kaempferi* stand in the *LK* area. Since the two study areas were contiguous, and because the vegetation in the deciduous broad-leaved stands in both areas were similar, we assumed that the characteristics of the

arthropods on the foliage of deciduous broad-leaved stands in the *CJ* area could be substituted for those in the *LK* area. On each of the two arthropod sampling dates, five branch-clipping samples were taken from *C. japonica*, five from *L. kaempferi*, and three from deciduous broad-leaved trees. Each sample consisted of two or three 60–80 cm long branches (leaves and associated twigs and branches) collected randomly from three trees from the coniferous stands, and two 30–40 cm long branches from 10 trees from the deciduous broad-leaved stands. Arthropod specimens from the understory were collected from each of the above three stands during one trial involving beating for 10 minutes in a 2×30 m quadrat. The data from the understories of the three stands were combined for the analysis. All branch-clipping and beating samples were treated immediately with an insecticide, scrutinized to collect all the arthropods (>1 mm) and then stored in 70% ethanol within 72 hours. These arthropods were identified, their body lengths were measured with a digital calliper or a micrometer under a binocular microscope, and then their individual dry weights were estimated by using equations (1)–(3) above. The density of arthropods was evaluated from the number or biomass per unit foliar mass for branch-clipping samples, while that for beating samples was evaluated in terms of the number or biomass per trial.

RESULTS

1) Foraging microhabitat

Significant differences in the use of five microhabitats were found between *Parus* species in the *CJ* area (extended Fisher's exact probability test, $\chi^2=32.75$, $df=4$, $P<0.001$), but not in the *LK* area ($\chi^2=1.92$, $df=4$, $P=0.75$) (see Table 1). The proportion of understory use did not differ significantly between *Parus* species nor between areas (Fisher's exact probability test, $P>0.05$ for each combination).

With respect to canopy layers, both *Parus* species used the foliage of deciduous broad-leaved trees more frequently than expected by chance in both areas (Table 1). *P. varius*'s preference for deciduous broad-leaved trees was much higher than that of *P. major* in the *CJ* area, but slightly lower in the *LK* area. Among the coniferous microhabitats, *P. major* used *C. japonica* in the *CJ* area and *L. kaempferi* in the *LK* area almost randomly, whereas *P. varius* scarcely used *C. japonica* in the *CJ* area but used *L. kaempferi* in the *LK* area almost at random.

Table 1. Foraging frequency and microhabitat selection in canopy layers by *P. major* and *P. varius* in each study area. The values of coverage for each transect and of foraging frequency are shown as percentages in parentheses. The selection ratio is defined as the ratio of the proportion of foraging frequency (except in the understory), to the proportion of microhabitat coverage. The χ^2 value was calculated after Manly et al. (1993). Levels of statistical significance were obtained after applying the Bonferroni correction. ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Foraging microhabitat	Coverage of transect [ha]	Foraging frequency	Selection ratio	χ^2 -value
<i>P. major</i>				
<i>CJ</i> area				
<i>C. japonica</i>	8.41 (54.6)	17 (53.1)	1.15	0.76 ^{ns}
<i>L. kaempferi</i>	0 (0.0)	1 (3.1)	—	—
deciduous broad-leaved trees	2.15 (14.0)	6 (18.8)	1.59	1.53 ^{ns}
others	4.83 (31.4)	3 (9.4)	0.35	5.15**
understory	—	5 (15.6)	—	—
<i>LK</i> area				
<i>C. japonica</i>	0.08 (0.5)	0 (0.0)	—	—
<i>L. kaempferi</i>	9.46 (63.3)	23 (52.3)	0.96	0.14 ^{ns}
deciduous broad-leaved trees	2.11 (14.1)	11 (25.0)	2.05	8.00**
others	3.30 (22.1)	4 (9.1)	0.48	3.42*
understory	—	6 (13.6)	—	—
<i>P. varius</i>				
<i>CJ</i> area				
<i>C. japonica</i>	8.41 (54.6)	11 (12.6)	0.25	58.68***
<i>L. kaempferi</i>	0 (0.0)	0 (0.0)	—	—
deciduous broad-leaved trees	2.15 (14.0)	64 (73.6)	5.72	315.43***
others	4.83 (31.4)	5 (5.7)	0.20	25.53***
understory	—	7 (8.0)	—	—
<i>LK</i> area				
<i>C. japonica</i>	0.08 (0.5)	1 (0.9)	—	—
<i>L. kaempferi</i>	9.46 (63.3)	62 (57.4)	0.98	0.08 ^{ns}
deciduous broad-leaved trees	2.11 (14.1)	26 (24.1)	1.84	12.62***
others	3.30 (22.1)	11 (10.2)	0.50	7.72**
understory	—	8 (7.4)	—	—

2) Composition and size distribution of prey items

In both study areas, *P. major* was always a single-prey loader, whereas *P. varius* carried multiple prey items at a time to its young. The number of prey items carried per visit by *P. varius* differed significantly between areas (Mann-Whitney U-test, $U = 9.96 \times 10^3$, $P = 0.02$) (Fig. 2).

The main nestling diet of both *Parus* species consisted of caterpillars and orthopteran insects (Fig. 3). The nestling diet of *P. varius* was dominated by caterpillars, which accounted for 76–94% (in number) of the whole nestling diet for each brood. In contrast, the main nestling diet of *P. major* comprised not only caterpillars (17–51%), but also orthopteran insects (42–75%; mainly Anoplophidae), and spiders (ca. 4%). The composition of *P. major*'s diet varied greatly between areas: the proportion of caterpillars in the diet was lower in number in the *CJ* area than in

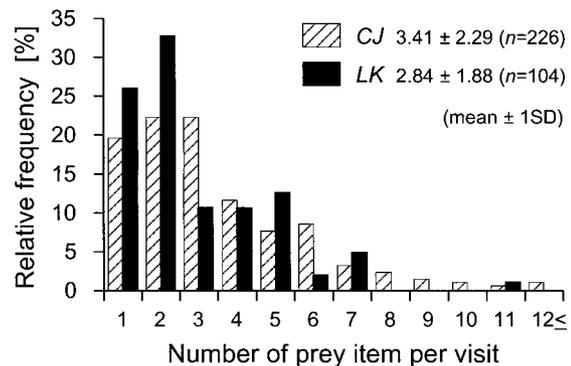


Fig. 2. Frequency distribution of the number of prey items per visit of *P. varius*.

the *LK* area. The composition of the nestling diet differed significantly between *Parus* species (G-test with Bonferroni correction, $G = 634.7$, $P < 0.001$ for

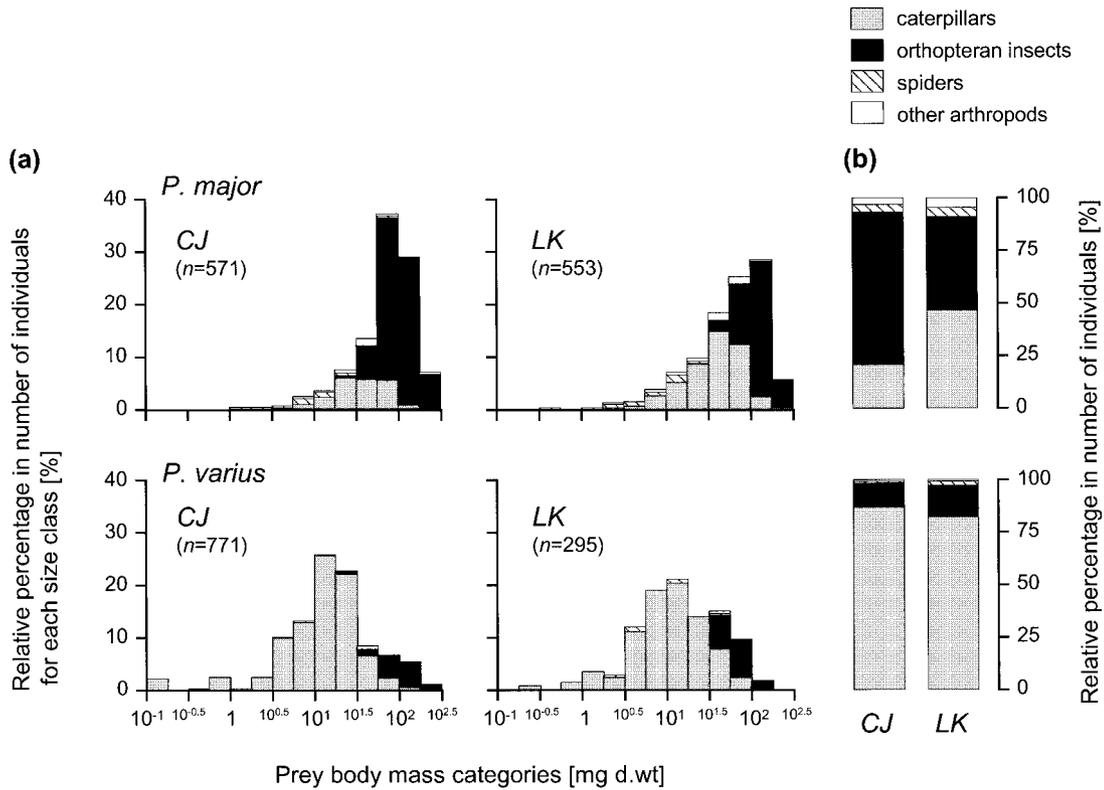


Fig. 3. Size distribution (a) and relative composition (b) of prey items used by *P. major* (upper) and *P. varius* (lower).

Table 2. Mean body mass (mean \pm 1 SD; mg dry wt) for all prey items and the major prey categories taken by *Parus major* and *P. varius* (sample sizes in parentheses). Levels of significance of differences in mean body mass, based on the Mann-Whitney U-test, are indicated (ns, $P > 0.05$; *, $P < 0.05$; ***, $P < 0.001$).

	Caterpillar	Orthoptera	All prey items
<i>P. major</i>			
CJ area	43.0 \pm 27.8	108.0 \pm 44.3	89.3 \pm 51.0
×	(119)	(414)	(571)
LK area	45.8 \pm 30.5	125.3 \pm 48.2	79.8 \pm 56.9
	(257)	(247)	(553)
<i>P. varius</i>			
CJ area	17.3 \pm 16.3	104.1 \pm 47.9	27.6 \pm 35.9
×	(671)	(91)	(771)
LK area	15.9 \pm 16.5	73.5 \pm 28.5	24.7 \pm 28.0
	(243)	(45)	(295)
<i>P. major</i> × <i>P. varius</i>			
CJ area	***	ns	***
LK area	***	***	***

CJ; $G=109.2$, $P < 0.001$ for LK) and between areas only for *P. major* (G -test with Bonferroni correction, $G=95.3$, $P < 0.001$ for *P. major*; $G=4.25$, $P=0.24$ for *P. varius*) (Fig. 3).

The minimum body mass of the prey items used by

Parus species was 0.1 mg d.wt (Fig. 3). *P. major* chose larger prey items than *P. varius* for all prey items (Table 2). The mean body mass of all prey items used by *P. major* differed significantly between areas (Mann-Whitney U-test, $U=1.37 \times 10^5$, $P <$

0.001). Prey items from 10¹ to 10^{2.25} mg d.wt accounted for ca. 90% of the nestling diet of *P. major*. The mean body mass of all prey items used by *P. varius* was smaller than that used by *P. major*, and did not differ between areas (U-test, U=1.07×10⁵, P=0.12). About 90% of the nestling diet of *P. varius* consisted of prey items ranging in dry weight from 10^{0.5} to 10² mg. The caterpillars taken by *P. major* did not differ in size between areas (U-test, U=1.45×10⁴, P=0.42), whereas those taken by *P. varius* did differ between areas (U-test, U=7.24×10⁴, P<0.01).

P. varius took prey of a broader range of size classes, for all prey items, than *P. major* (Table 3). The difference in the breadth of prey size was smaller between areas than between species. The overlap in the prey-body-size distribution was larger between areas than between *Parus* species (Table 4). The same results were found for caterpillars, but not for Orthoptera.

The smaller difference in the breadth, and the larger overlap for prey size, between areas than between species, suggests that both *P. major* and *P. varius* had specific prey size class preferences.

3) Composition and size distribution of arthropods in foraging microhabitats

The number of individuals of arthropods larger than 0.1 mg d.wt accounted for 94% of all individu-

Table 3. Breadth of the size class distribution for all prey items and the major prey categories (H').

	Caterpillar	Orthoptera	All prey items
<i>P. major</i>			
CJ area	1.58	1.19	1.62
LK area	1.67	1.08	1.83
<i>P. varius</i>			
CJ area	1.86	1.31	2.05
LK area	1.92	0.96	2.05

Table 4. Overlap of the size-class distribution for all prey items and the major prey categories (α).

	Caterpillar	Orthoptera	All prey items
Overlap between areas (CJ×LK)			
<i>P. major</i>	0.97	0.91	0.96
<i>P. varius</i>	0.95	0.71	0.93
Overlap between bird species (<i>P. major</i> × <i>P. varius</i>)			
CJ area	0.64	0.99	0.40
LK area	0.56	0.49	0.54

als. The number of individuals and biomass of all arthropods was highest in deciduous broad-leaved trees and lowest in *C. japonica* (Table 5).

The mean body mass of major prey categories (caterpillars, orthopteran insects and spiders) also differed among foraging microhabitats (Table 6). The caterpillars on *L. kaempferi* foliage were significantly smaller than those on deciduous broad-leaved tree foliage or in the understory. The spiders obtained from *C. japonica* foliage were significantly smaller than those in the three other foraging microhabitats were. The mean body mass for all major prey categories was largest in *C. japonica* foliage, where a large orthopteran insect occurred, whereas mean body mass was smallest in *L. kaempferi* foliage, which was dominated by small caterpillars and spiders. These major prey types contributed relatively large proportions of the whole arthropod fauna: 28.1% (understory)—42.7% (*C. japonica*) in terms of individuals, and 15.8% (*C. japonica*)—38.2% (deciduous broad-leaved trees) in terms of biomass (Fig. 4).

The composition and size distribution of arthropods differed between foraging microhabitats (Fig. 4). The size class of caterpillars most frequently observed in *L. kaempferi* (10^{-0.5}–10^{0.25} mg d.wt) was smaller than that found in deciduous broad-leaved trees (10^{0.5}–10^{1.25} mg d.wt). In the understory, caterpillars of various sizes (10^{-0.75}–10^{2.25} mg d.wt) occurred. Orthopteran insects contributed only 1.4% of the whole arthropod fauna in terms of numbers of individuals, but contributed 13% of the biomass in *C. japonica* owing to the occurrence of one large indi-

Table 5. Numbers of individuals and biomass of arthropods (>0.1 mg dry wt) taken by *Parus major* and *P. varius* in each foraging microhabitat (mean±1 SD). The different letters following values in canopy samples indicate significant differences between mean values according to the Steel-Dwass test (P<0.05).

	Number of individuals ¹	Biomass ²
Canopy		
<i>C. japonica</i>	34.6±11.3 ^a	511.4±481.8 ^a
<i>L. kaempferi</i>	429.1±142.2 ^b	2207.0±1758.5 ^b
deciduous broad-leaved trees	1626.0±1277.0 ^c	7933.4±7046.8 ^b
Understory	212.8±57.5	875.4±173.2

¹Number of individuals and ²biomass (mg dry wt) per unit foliar mass (kg⁻¹ dry wt) for the canopy or per trial for the understory

Nestling-diet of two *Parus* species

Table 6. Mean body masses (mean ± 1 SD; mg dry wt) of prey in each foraging microhabitat (sample sizes in parentheses). The different letters following values indicate significant differences in the mean body mass between foraging microhabitats according to the Steel-Dwass test ($P < 0.05$).

	Caterpillar	Orthoptera ¹	Spider	All major prey categories
Canopy				
<i>C. japonica</i>	5.0 ± 7.4 (3) ¹	139.9 (2)	0.7 ± 1.3 (56) ^a	5.5 ± 35.3 (61) ^a
<i>L. kaempferi</i>	2.7 ± 3.8 (98) ^a		0.9 ± 1.0 (56) ^b	2.0 ± 3.2 (154) ^b
deciduous broad-leaved trees	6.8 ± 6.2 (84) ^b	2.2 ± 1.1 (5)	1.7 ± 3.5 (53) ^b	4.7 ± 5.8 (142) ^c
Understory	8.4 ± 15.1 (102) ^b	16.7 ± 23.0 (11)	1.4 ± 2.1 (246) ^b	3.8 ± 9.9 (359) ^b

¹ No statistical analysis was performed because of the small sample size.

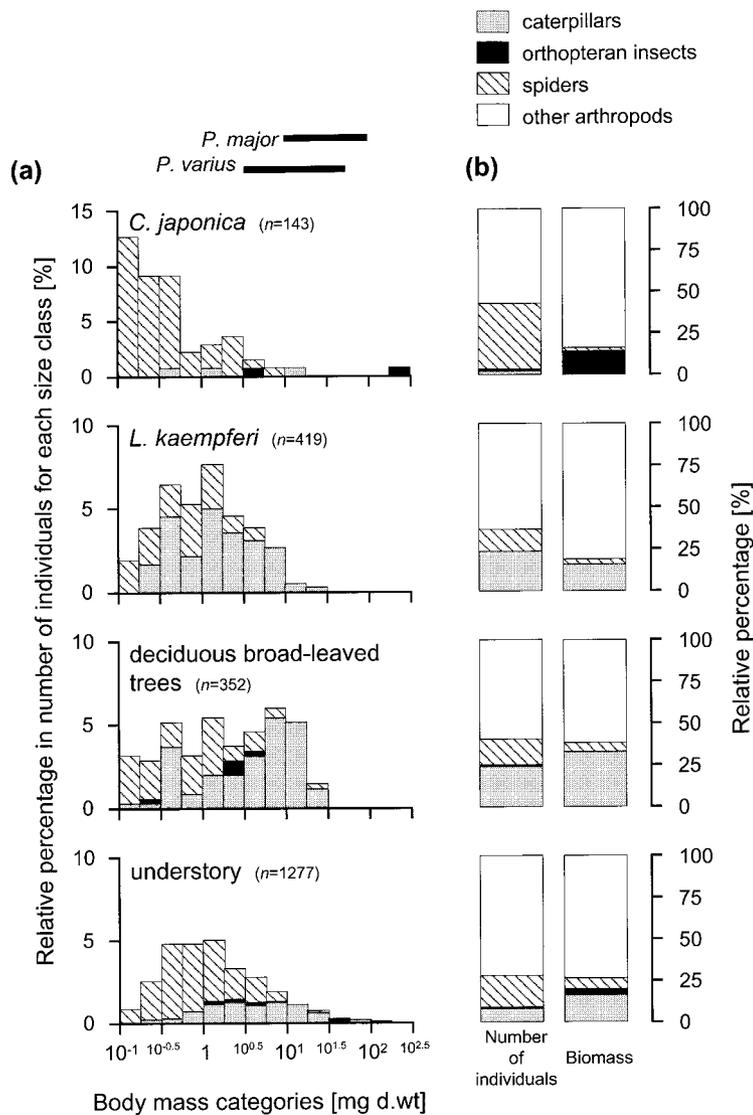


Fig. 4. Size distribution (a) and relative composition in number of individuals and biomass (b) of arthropods collected from each foraging microhabitat. Only arthropods larger than the minimum size of prey items are shown. The horizontal bar above (a) shows the size range containing 90% of caterpillars preyed on by *P. major* and *P. varius*.

vidual (276 mg d.wt). Spider was the most dominant group in number of individuals in all microhabitats, but most of them were less than $10^{0.25}$ mg d.wt.

DISCUSSION

1) Prey size as a contributory factor of nestling-diet selection in two *Parus* species

In this study, two *Parus* species selectively chose prey items of a particular size range specific to each species. The differences in the mean body mass of prey used by each *Parus* species in two study areas were markedly smaller than those between *Parus* species (Table 2). The inter-area differences in the breadth of prey size used by each *Parus* species was small (Table 3) and the inter-area overlap was large (Table 4) in spite of large differences in the body-size distribution (Fig. 4) and other characteristics (Tables 5 and 6) of arthropods between areas. It appears from these results that prey size is more important than prey species for diet selection by these *Parus* species.

The difference in prey size in the diet between sympatric *Parus* species (Table 2) may be due to food-resource partitioning for a relaxation of interspecific competition. Several authors have reported that preferred prey size differs among *Parus* species (Betts 1955; Gibb & Betts 1963; Eguchi 1985). Sympatric *Parus* species tend to vertically segregate their foraging microhabitats during the non-breeding season (Perrins 1979), and it is also reported that vertical partitioning between *P. major* and *P. varius* did not occur during the breeding season (Nakamura 1970). As reported in Nakamura (1970), the vertical partitioning between those *Parus* species was not found in our study. Because both species preferred deciduous broad-leaved trees, there may have been local competition for foraging microhabitats between them. Nevertheless, they may have been able to avoid competitive interactions by taking different-sized prey.

Food requirements by birds are strongly correlated with their body mass (Nagy 1987). Since the body mass of the two *Parus* species is almost the same (16.5 g fresh weight (f.wt) for *P. major* and 17.0 g f.wt for *P. varius*; Yui 1988), both *Parus* species should have similar feeding efficiencies. The interspecific difference in prey-size preference could be explained by the fact that whereas *P. major* is always a single-prey loader, *P. varius* is a multiple-prey loader (Fig. 2). *P. varius* may compensate for a decrease in its feeding efficiency by carrying many small prey items at a time.

2) Matching of foraging microhabitat use by *Parus* species with the characteristics of the arthropod community

The characteristics of arthropods as potential prey, such as abundance, biomass (Table 5) and the composition and size distribution of individuals (Table 6, Fig. 4), greatly differed among foraging microhabitats. One of the strategies used by *Parus* species to adapt to mosaic environments with various vegetation types and varying food availability, is selective use of foraging microhabitats with food resources sufficient for reproduction (cf. Dias & Blondel 1996).

Considerable numbers of caterpillars occurred in each foraging microhabitat except in the foliage of *C. japonica*, but their body-size distribution differed among microhabitats (Fig. 4). Orthopteran insects were found in each microhabitat except the foliage of *L. kaempferi* (Fig. 4). In number, their contribution to the whole arthropod fauna was very small, but their contribution to biomass was large because a few large individuals occurred. In this study, the sample size for the branch clipping method may have been insufficient to evaluate the exact abundance and size distribution of orthopteran insects on trees, because of low efficiency of sampling. Our results were similar, nevertheless, to those based on chemical-knockdown samples, which showed that the proportion of orthopteran insects was less than 1% in number, but 16% in biomass (average for the data of June and August; Hijii 1989). Because small orthopteran insects were found both in the foliage of deciduous broad-leaved trees and in the understory, larger individuals may also inhabit both microhabitats. Previously, chemical-knockdown sampling had failed to find orthopteran insects in the foliage of *L. kaempferi* (Terakawa unpubl. data), a fact confirmed by our results. Although spiders have been reported as a secondary major food resource of *Parus* species in many habitats (e.g. Gibb & Betts 1963; Won et al. 1965; Minot 1981; Eguchi 1985; Arakida 1995), they were not a preferred nestling food in our study (Fig. 3). This is probably because small individuals constituted a large proportion of the spiders in number in this study site.

There were significant differences in the use of foraging microhabitats between *Parus* species in the *CJ* area, but not in the *LK* area (Table 1). Both *Parus* species selectively used the foliage of deciduous broad-leaved trees as a foraging microhabitat in both areas. In deciduous broad-leaved trees, various-sized caterpillars available to both *P. varius* ($10^{0.5}$ – $10^{1.75}$)

and *P. major* (10^1 – 10^2) contributed large proportions to the arthropod fauna (Fig. 4). Thus, the foliage of deciduous broad-leaved trees would have been important for both *Parus* species in providing stable food resources. Moreover, there may be more advantageous to *P. varius* capable of using smaller caterpillars, because smaller prey items were abundant, which may enhance the food availability to *P. varius* in this foraging microhabitat (Fig. 4). Thus, *P. varius* could use caterpillars as its main food category (Fig. 3) in both areas.

The foliage of *C. japonica* was mainly used by *P. major*, but only scarcely used by *P. varius* (Table 1). Although the availability of caterpillars was very low, there were large orthopteran insects in the foliage of *C. japonica* (Fig. 4). For *P. major*, which tended to prefer large prey items (Table 2, Fig. 3), orthopteran insects on *C. japonica* trees can be a suitable food resource, even if their abundance is low (Table 1).

In the LK area, both *Parus* species randomly used the foliage of *L. kaempferi*, the preferences for which were lower than for deciduous broad-leaved trees (Table 1). The contribution of individual caterpillars to the overall arthropod fauna was almost the same, but the body-size distribution differed between these microhabitats. The profitability for *P. major* may be lower in *L. kaempferi*, because the proportion of small caterpillars was relatively high. Moreover, both species may not prefer coniferous *L. kaempferi* as much as deciduous broad-leaved trees owing to their morphological adaptations (Nakamura 1978).

In both areas, both *Parus* species also foraged from the understory (about 10% of foraging behavior) (Table 1), where suitable caterpillars and orthopteran insects were available for both *Parus* species (Fig. 4). This foraging microhabitat would also be a useful food source for both *Parus* species.

In conclusion, both *Parus* species selectively used foraging microhabitats with different arthropod communities according to their species-specific size preferences. The composition of their diets may reflect both the characteristics of the arthropod community in each area and the abundance and size of prey items in each foraging microhabitat within each area.

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