

Foraging mode shifts of four insectivorous bird species under temporally varying resource distribution in a Japanese deciduous forest

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Abstract Temporal changes in the foraging habitat of four forest bird species and the distribution pattern of arthropod populations were investigated. The abundance and distribution of arthropods changed drastically with the season within the forest. Lepidoptera larvae were most abundant in the canopy in the first three weeks after budbreak; their numbers decreased rapidly during mid-June. In contrast, on the forest floor, the larvae were abundant from early to late June. The foraging height of the Narcissus Flycatcher *Ficedula narcissina* changed in parallel with the distribution pattern of Lepidoptera larvae. Three other species, the Great Tit *Parus major*, Marsh Tit *P. palustris*, and Eastern Crowned Warbler *Phylloscopus coronatus*, however, did not change their foraging heights; they continued to forage in the canopy. These differences are probably due to the greater preference of the flycatcher for Lepidoptera larvae compared with the other three species. The three other species switched from feeding on Lepidoptera larvae to spiders or other arthropods in mid June, when the number of Lepidoptera larvae decreased in the canopy. The results of this study suggest that the abundance and distribution of arthropods and differences in foraging tactics among bird species considerably affect avian foraging habitat. The foraging behavior of three species of forest birds revealed species-specific responses to spatio-temporal fluctuations in the distribution of resources.

Key words Forest bird, Foraging tactics, Lepidoptera larvae

Since Lack's (1971) findings of a clear-cut partitioning of foraging substrates in tree crowns among tit species, other studies have confirmed a close relationship between bird foraging habit and resource distribution (Alatalo 1980; Holmes & Schultz 1988). Forest bird species have been shown to co-exist by partitioning their food resources by segregating their foraging habitats (MacArthur 1958; Lack 1971; Schoener 1974). However, studies of forest avian communities have usually been conducted under rather stable circumstances (Wagner 1981; MacNally 1994). The spatio-temporal variation in resource distribution can considerably affect the foraging behaviors of birds, and hence bird communities (Wiens 1989; Maurer 1990).

In reality, the distribution of food resources for in-

sectivorous birds within a forest change drastically with the season (Raupp et al. 1988; Hunter 1991). In temperate deciduous forests, the abundance and distribution of herbivorous insects, in particular Lepidoptera larvae, which are the most preferred prey of insectivorous forest birds (Royama 1969), change dramatically in spring due to strengthening defence traits of tree leaves after budbreak (Feeny 1970; Murakami & Wada 1997). Moreover, most bird species require greater resources for feeding their nestlings and fledglings in this season (Holmes et al. 1979; Burke & Nol 1998). It has also been concluded that food often limits the reproduction and survival of forest birds during their breeding season (Martin 1987; Rodenhouse & Holmes 1992). It is, therefore, expected that temporal changes in foraging behavior among birds in response to the abundance and distribution of arthropods should affect the fitness of individual birds, and hence the structure of the avian community. Although van Noordwijk et al. (1995)

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suggested a relationship between the timing of Great Tit breeding and the availability of Lepidoptera larvae as food for their fledglings, the responses of birds to temporal changes in resource abundance and distribution have been little studied. Further understanding of species-specific responses of birds to temporal changes in resource abundance and distribution in deciduous forests in spring will help to explain the composition of local bird communities (cf. Holmes et al. 1979; Robinson & Holmes 1982; Hino 1994).

Hejl and Verner (1990) suggested that some species of birds living in the same habitat undergo similar changes in foraging behavior and diet as temporal changes affect resource abundance and distribution. In this study, I hypothesized that all forest bird species change their foraging habitat according to the distributional changes in Lepidoptera larvae. To evaluate this hypothesis, I measured the abundance and distribution of arthropods within a forest during spring and early summer and quantified the differences in the foraging behavior of four forest bird species, Great Tit *Parus major*, Marsh Tit *P. palustris*, Narcissus Flycatcher *Ficedula narcissina*, and Eastern Crowned Warbler *Phylloscopus coronatus*, in response to the changes in resource distribution.

STUDY AREA AND METHODS

Field studies were performed in a 9 ha (300 × 300 m) plot in Tomakomai Experimental Forest (TOEF) of Hokkaido University in northern Japan (42°43'N, 141°36'E; 50–95 m elevation). Oak *Quercus crispula*, maple *Acer mono*, and linden *Tilia japonica* dominate the vegetation of the study plot. A 20-m square grid was set up on the forest floor using color markers. The buds of the deciduous trees opened in mid May. Two resident insectivorous bird species, the Great Tit and the Marsh Tit, began to brood in mid May, and two migrant bird species, Narcissus Flycatcher and Eastern Crowned Warbler, began to brood in late May (cf. Ishigaki & Matsuoka 1972). Fledgling Great Tits and Marsh Tits were observed to leave their nests during late May and early June, and those of Narcissus Flycatcher and Eastern Crowned Warbler, during early and mid June. Secondary nests were built by two pairs of Great Tit in the study area.

Within the study plot, I measured the vertical foliage distribution on 8 July, 1995. The presence or absence of foliage above each of the color markers

($n=256$) for bird observation grids was recorded for each of the following height layers: 0–0.5 m, 0.5–1.5 m, 1.5–3 m, 3–5 m, 5–7 m, 7–10 m, 10–15 m, 15–20 m, >20 m). The percentage of foliage present in each layer, P_i , was calculated as $P_i = (p_i/256) \times 100\%$, where p_i is the number of observation points above which foliage is present at the i th height layer. The canopy top was 15 to 25 m high, and saplings and current year seedlings of the dominant tree species grew in the shrub layer (0–1.5 m). The foliage was rather sparse at 1.5–5 m under the dense foliage at 7–15 m.

Sampling of arthropods. To reveal the seasonal changes in arthropod distributions in the canopy trees (canopy) and in the understory vegetation (forest floor), two different sampling methodologies were conducted simultaneously in the forest around the bird observation plot. Arthropods in the canopy were collected using the beating method, and those on the forest floor were collected by sweeping.

One individual of oak was chosen randomly for each sampling period. The oak canopy was sampled weekly from 25 May to 6 July 1995. Climbing to the canopy layer (10–25 m high) using Perry's (1978) method, I beat branches repeatedly, and collected arthropods which dropped onto a tray (80 × 80 cm) beneath the branches. This was replicated randomly ten times for different parts of an individual tree. For each sample, I selected a single tree that had not previously been sampled.

Arthropods on the forest floor were collected by sweeping every week from 1 June to 13 July. For each sample, a 40 cm diameter insect net was swept continuously for 30 min. within a 400 m² square on the forest floor. The same area was sampled only once during the study period. The arthropods collected were classified into two categories, Lepidoptera larvae and other arthropods, and the number of individuals was counted separately for each category.

Bird foraging ecology. Individuals of the four dominant bird species were identified by color rings, and their foraging behavior was observed for five consecutive days each week during the breeding season from 24 May to 5 July 1995. An observer walked through the study plot on a systematic basis (cf. Kendigh 1944) from 05:00 to 11:00 hr. No more than 10 foraging maneuvers for each individual bird encountered were observed, these included both feeding for nestling or fledglings and foraging for themselves. The feeding of nestlings or fledglings ac-

counted for about 80% of all foraging maneuvers. On average, an individual bird was observed continuously for 3.5 min. during which it averaged 6.2 foraging maneuvers. Whenever the individual bird being observed made a foraging maneuver, the height at which it foraged, the prey type (Lepidoptera larvae or other arthropods), the kind of attack (sallying, gleaning, or pecking, and the substrate were recorded; cf. Holmes et al. 1979). Foraging heights were estimated to the nearest two metres. An individual previously observed on the same day was left out so as to avoid a bias due to a particular individual. The kinds of attacks and substrates were combined into seven different foraging behaviors: 1) Air Sally, 2) Leaf Sally, 3) Leaf Glean, 4) Leaf Pecking, 5) Twig and Trunk Sally, 6) Twig and Trunk Glean, and 7) Twig and Trunk Pecking. The daily mean height of the foraging site was calculated for each individual bird. The percentage of foraging on Lepidoptera larvae (Prey Type) and those of each foraging method were calculated for each day. The daily data were summed for each week of the survey period.

Statistical analyses. A two-way ANOVA (factor=period, arthropod category) was used to reveal seasonal changes in the abundance of the two arthropod categories in the canopy. The weekly changes and inter-specific differences in the foraging height and the proportion of Lepidoptera larvae in bird prey was analyzed by two-way ANOVA (factor=time, bird species). Furthermore, the seasonal and inter-specific difference in foraging behavior was analyzed by a two-way MANOVA (factor=time, species) based on the frequencies of each foraging method. Exact values were \log_{10} transformed and percentage data were arc-sin transformed to standardize variances and improve normality, if necessary to satisfy the assumptions of the ANOVAs. All statistical tests were two-tailed. In all cases, statistical significance was evaluated at $P < 0.05$.

RESULTS

Arthropod distribution. A two-way ANOVA revealed significant effects of both sampling period ($F = 12.84$, $df = 6$ and 126 , $P < 0.001$) and arthropod category ($F = 4.20$, $df = 1$ and 126 , $P = 0.043$; Fig. 1a). The interaction effect was also significant ($F = 4.25$, $df = 6$ and 126 , $P = 0.002$). The number of Lepidoptera larvae showed a conspicuous peak during late May to mid June. Thereafter, it decreased rapidly and remained at a low level from late June to July. The

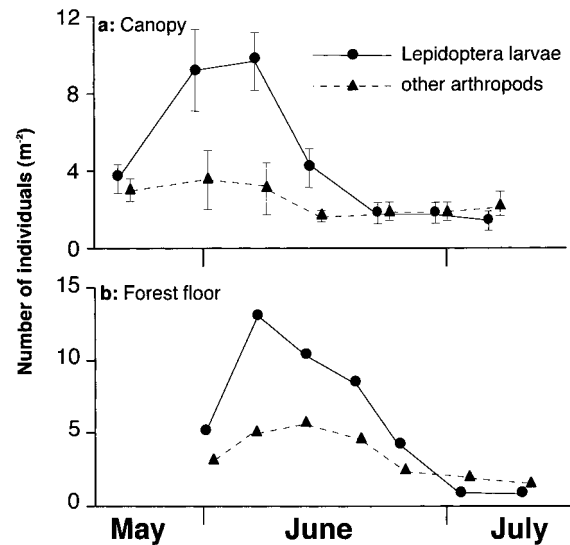


Fig. 1. Seasonal changes in the numbers of arthropods in the canopy (a), and on the forest floor (b). Solid lines indicate Lepidoptera larvae and dotted lines other arthropods. Error bars are standard errors of the means.

number of other arthropods showed a smaller peak than that of the Lepidoptera larvae from late May to early June. The number of Lepidoptera larvae was larger than that of other arthropods from late May to mid June.

On the forest floor, the number of Lepidoptera larvae peaked in early June, then gradually decreased and reached a low level in late June (Fig. 1b). The number of other arthropods showed a rather small peak in mid June.

Bird foraging habitat. In the study plot, 11 individual Great Tits, 16 Marsh Tits, 21 Narcissus Flycatchers, and 19 Eastern Crowned Warblers were recorded during the study period. Foraging height varied significantly seasonally ($F = 6.47$, $df = 5$ and 15 , $P < 0.001$; Fig. 2b) and among bird species ($F = 137.0$, $df = 3$ and 15 , $P < 0.001$) with significant interaction ($F = 7.95$, $df = 18$ and 15 , $P < 0.001$). Great Tits, Marsh Tits, and warblers continued to forage in the canopy throughout the study period, whereas flycatchers changed their foraging height. Flycatchers foraged in the canopy from late May to mid June, then on the forest floor from mid June to late June, and again in the canopy from late June to early July.

Prey types were identified in 68% of the 3,857 foraging maneuvers observed. The prey type varied significantly seasonally ($F = 64.96$, $df = 5$ and 96 , $P < 0.001$; Fig. 3) and among bird species ($F = 5.647$, $df = 3$ and 96 , $P = 0.0013$) with significant interaction

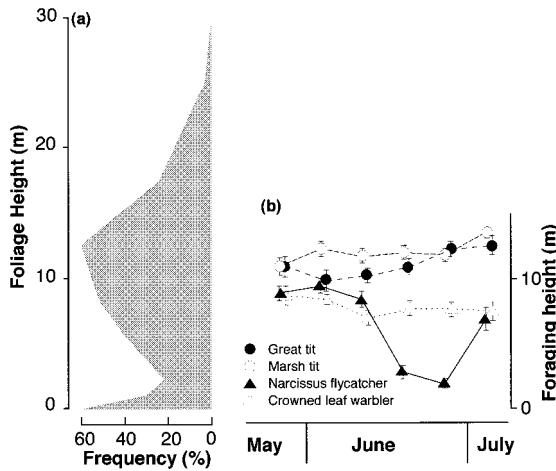


Fig. 2. Vertical foliage distribution in the study plot (a), and seasonal changes in the foraging height of four-bird species (b). Error bars are standard errors of the means.

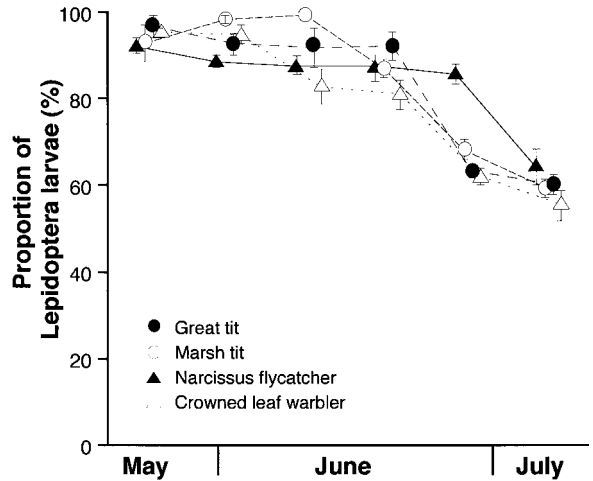


Fig. 3. Seasonal changes in the proportion of Lepidoptera larvae preyed on by four bird species. Error bars are standard errors of the means.

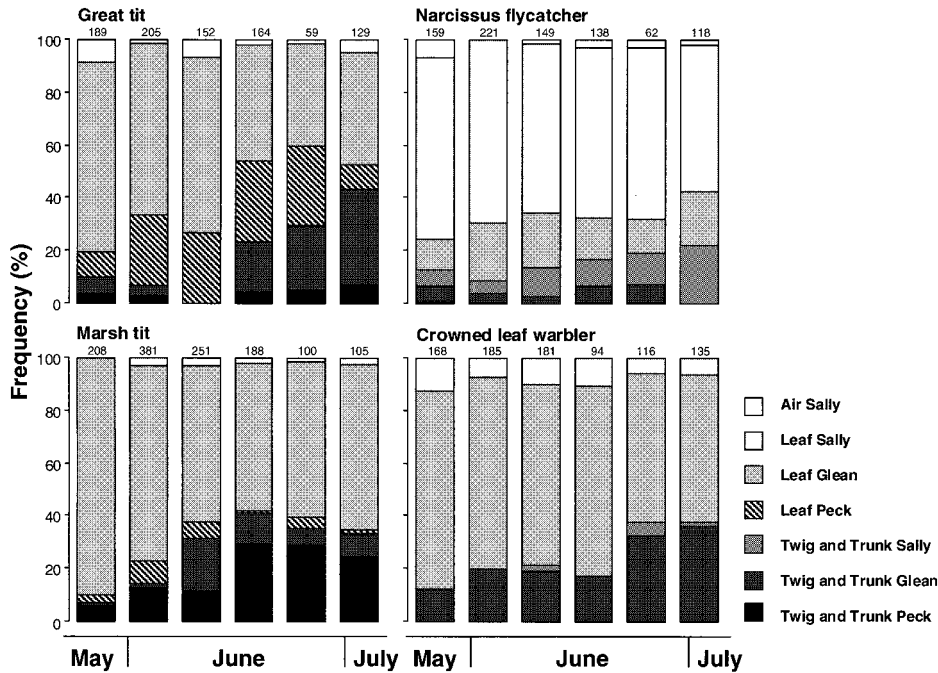


Fig. 4. Seasonal changes in relative frequencies of each of the foraging behaviors employed by four bird species. The letters on the top of each bar were the numbers of observation for each bird species in each period.

($F=4.371$, $df=15$ and 96 , $P<0.001$). From late May to mid June, all four bird species foraged mostly on Lepidoptera larvae. In late June, the flycatchers continued to forage on Lepidoptera larvae, whereas the three other species reduced their utilization ratio of Lepidoptera larvae. Then in July, all four species utilized the Lepidoptera larvae at a ratio of about 60%.

The MANOVA analysis revealed that foraging behavior differed both among bird species (Hotelling-

Lawley Trace: bird species, value=12.77, $F=53.94$, $df=21$, $P<0.001$) and across the seasonal period (value=1.669, $F=2.176$, $df=35$, $P<0.001$; Fig. 4) with significant interaction (value=1.667, $F=1.404$, $df=105$, $P=0.008$). Flycatchers mostly foraged by sallying from leaves throughout the study period (more than 60% of all foraging maneuvers) and rarely utilized twigs and trunks (<15%). The three other species frequently foraged by gleaning from

leaves. Great Tit also foraged by pecking on leaf rolling caterpillars, and Marsh Tit by pecking on twigs and trunks. From late June to July, these three species came to forage more frequently on twigs and trunks (about 40%) than in the previous period (about 20%).

DISCUSSION

Lepidoptera larvae were abundant in the oak canopy from late May to mid June, and then rapidly decreased. The spring foliage is known to open a “window” of high quality leaves for herbivorous insects but only for a short duration, which causes changes in the abundance and distribution of herbivorous insects (Feeny 1970; Kraft & Denno 1982; Murakami & Wada 1997). In the present study, Lepidoptera larvae disappeared rapidly from the canopy after early June, but became abundant on the forest floor during early to mid June. Many Lepidoptera larvae are known to migrate from the canopy to the floor for pupation or to seek alternative food resources when canopy leaves strengthen their defence traits during this season (Murakami & Wada 1997). In contrast, other arthropods, most of which are not herbivores (e.g. spiders and dipterans), did not make such a drastic distributional change.

The present study showed that Narcissus Flycatchers shifted their foraging height nearly in parallel with the change in distribution of Lepidoptera larvae. They foraged in the canopy from late May to early June, then on the forest floor from mid to late June, confirming the results of my previous study conducted in 1994 (Murakami 1998). Such a shift was nearly synchronous with the decline in Lepidoptera larvae biomass in the canopy, but a little later than the peak of larval abundance on the forest floor, thus implying that the foraging habitat shift was due to the decline of Lepidoptera larvae in the canopy rather than the increase of the larvae on the floor. The three other bird species, however, continued foraging in the canopy even after this critical moment. During this study, Narcissus Flycatchers foraged intensively on Lepidoptera larvae, shifting their foraging site from the canopy to the forest floor in late June, when the abundance of larvae in the canopy decreased. In contrast, the three other bird species continued to forage in the canopy, but shifted their foraging substrate there from leaves to twigs or trunks, and shifted their main prey from Lepidoptera larvae to other arthropods. Thus, the Narcissus Flycatcher and the three

other bird species coped differently with the abrupt change in the abundance of Lepidoptera larvae as the most important food resource in the canopy.

The different responses among these four species should correspond to their species-specific foraging tactics. Rosenberg (1993) suggested that the foraging tactics utilized by birds considerably affect the accessibility of prey organisms on different substrates. Moreover, it has been suggested that differences in foraging methods affect a bird's prey-type selection and that gleaners can obtain smaller prey than sallyers (Holmes & Recher 1986). In this study, the flycatcher mainly performed sallies, whereas the other species frequently fed by gleaning or pecking. The flycatcher probably changed its foraging habitat after having difficulty in finding alternative food resources in the canopy during mid and late June when Lepidoptera larvae, which are far larger than other available arthropods within the forest (Murakami unpubl. data), disappeared from the canopy. The three other species, however, did not change their foraging layer in this season. Instead, they began to frequently utilize other arthropods as alternative resources. In early July, the flycatcher resumed foraging in the canopy. When the density of Lepidoptera larvae was low both in the canopy and on the forest floor, the flycatcher, due to its innate foraging behavior (Wiens 1984), probably foraged more efficiently in the canopy than on the floor. Because the fledglings of all four bird species had already left their nests by this season, breeding phenology should have little or not effect on the differences observed in foraging site selection.

The presence of species that prey on birds can also affect the foraging site selection of birds (Székely et al. 1989). A location that is covered by foliage may be safer than an exposed one (Ekman 1987). In the study plot, Japanese Lesser Sparrowhawk *Accipiter gularis* was observed five times during the study period (Murakami pers. obs.). The ground layer (0–5 m) of this forest was not densely covered by foliage (Fig. 2), which indicates that birds on the ground may be at greater risk of predation by birds. Therefore, it is expected that Narcissus Flycatchers selected a rather risky habitat in order to be able to forage on Lepidoptera larvae. Interspecific competition among bird species may also affect foraging habitat selection (Alatalo et al. 1987). Although there was no direct evidence for interspecific competition in this study, the differences in foraging heights among the four bird species (Fig. 2) may indicate that interspecific competition was operating.

Given that previous studies have shown that seasonal shifts in foraging mode coincide among different bird species in the same habitat due to the change in prey availability (Alatalo 1980; Rotenberry & Wiens 1980; Hejl & Verner 1990), I hypothesized that all four bird species tracked the distributional change in Lepidoptera larvae. My results, however, indicated that each bird species responds differently to the changes in resource distribution according to their foraging tactics, which may be limited by their species-specific morphological structure as shown by Moreno and Carrascal (1993). Further investigation of the relations between such versatile foraging behaviors of birds and fluctuation of resource abundance and distribution will provide a deeper insight into the mechanisms of species co-existence in bird communities (cf. Smith & Rotenberry 1990).

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