



HOKKAIDO UNIVERSITY

Title	Trophic Interactions among Insectivorous Birds, Herbivorous Insects, and Plants in Temperate Deciduous Forest
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Degree Grantor	北海道大学
Degree Name	博士(地球環境科学)
Dissertation Number	甲第4511号
Issue Date	1998-03-25
DOI	https://doi.org/10.11501/3137227
Doc URL	https://hdl.handle.net/2115/32517
Type	doctoral thesis
File Information	4511.pdf



**Trophic Interactions among Insectivorous Birds,
Herbivorous Insects, and Plants
in Temperate Deciduous Forest**

A Dissertation Submitted to
Division of BioScience,
Graduate School of Environmental Earth Science,
Hokkaido University
for the Degree of Doctor

by

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1997

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Abstract

Trophic interactions among insectivorous passerine birds, carnivorous and herbivorous insects, and plants (oak) were studied in temperate deciduous forests, focusing on the variability and versatility in each component.

In Chapter I, indirect effects of strengthening plant defenses on bird foraging behaviors via herbivorous insects, in particular, lepidopterous larvae, were studied. I investigated seasonal changes in leaf characteristics related to the defense system against herbivorous insects, distribution of arthropod populations, and foraging behaviors of four bird species, great tit (*Parus major*), marsh tit (*Parus palustris*), narcissus flycatcher (*Ficedula narcissina*), and crowned willow warbler (*Phylloscopus occipitalis*), in a temperate deciduous forest in northern Japan.

During a relatively short period after the budbreak, leaf toughness and tannin content of oak leaves increased, while nitrogen and water contents decreased.

The biomass of lepidopterous larvae in the canopy was large in early spring, three weeks after the budbreak, but decreased rapidly in mid June. In contrast, the larvae became abundant on the forest floor from early to late June. A rearing experiment showed that one of typical spring-feeding lepidopterous species, *Conistra unimacula* (Noctuidae), could not grow up to the 6th (last) instar if reared only on canopy leaves. However, when the food was changed from canopy leaves to seedling leaves after the 4th instar, 72% of the larvae could survive through the 5th instar, and 30% pupated. Seedling leaves were softer, fresher, and more nutritious than canopy leaves. These differences in leaf quality improved the performance of larvae reared on seedling leaves. These findings suggest that lepidopterous larvae

migrate from the oak canopy to the forest floor in late spring not only to pupate in the ground but also to seek alternative food resources on the forest floor. Thus, strengthening of defense traits in canopy leaves caused changes in the abundance and distribution of lepidopterous larvae.

Narcissus flycatchers foraged in the canopy from late May to mid June but on the ground from late June, mostly preferring lepidopterous larvae (about 80% of the total prey items). The other species, great tit, marsh tit, and crowned willow warbler, however, did not change their foraging heights; they continued to forage in the canopy. This difference is probably due to the greater preference of the flycatcher for lepidopterous larvae compared with the other species. The other species changed their prey from lepidopterous larvae to spiders or other arthropods in mid June, when the number of lepidopterous larvae decreased in the canopy. Thus, the studied bird species showed the specific responses to the spatio-temporal variation in the resource abundance and distribution.

Foraging behaviors of insectivorous birds were indirectly affected by plants through herbivorous insects.

In Chapter II, two field experiments were performed to detect effects of avian predation on the lower trophic levels.

First, to assess effects of avian predation on leaf-rolling lepidopterous larvae, birds were excluded from Japanese lilac (*Syringa reticulata*) trees by covering them with nets. Only one species, *Zelleria* sp. was reduced in number by avian predation: no effect of birds was detected in pylarid species. This is probably due to the differences in the shape of leaf roll. *Zelleria* sp. alters the leaf form greater than the other species, so that birds can detect the rolls more easily. The shape of leaf roll or the degree of alteration of leaf arrangement may be a compromise among adaptations to different stresses, plant resistance, parasitism and/or predation by arthropods and

birds. Of the four predominant insectivorous species, great tit and marsh tit, intensely visited the lilac to forage on leaf rollers, but narcissus flycatcher and crowned willow warbler did not. This is probably due to the differences in their foraging methods.

Next, to determine effects of foliage gleaning bird (great tit) and bark gleaning bird (nuthatch) on organisms at lower trophic levels, I manipulated their presence or absence within a large canopy enclosure. This experiment detected effects of the two bird species on lepidopterous larvae, ants, and the degree of leaf damage of oak (*Quercus crispula*) leaves. Great tit reduced the abundance of lepidopterous larvae and eventually the degree of leaf damage. On the other hand, nuthatch reduced the abundance of ants, but did not affect the abundance of lepidopterous larvae and the degree of leaf damage. Effects of ants on lepidopterous larvae were also convinced. These results indicate that insectivorous birds play different roles in forest ecosystems according to their species-specific natures of foraging behaviors.

General Introduction

Ecologists have long been interested in the importance of interactions between trophic levels in determining distribution and abundance of organisms and hence community structure (Strauss 1991; Hunter and Price 1992; Wootton 1992).

Recently, attention has been drawn toward the relative importance of direct effects (effects of one species on another as a consequence of a physical interaction between the two) and indirect effects (effects that are not the result of a physical interaction but are operated via a third species) of species interactions on community structure (Wootton 1992; Menge et al. 1996). However, indirect effects have been less studied than direct effects, perhaps because indirect effects are often considered to be unimportant compared to direct interactions (cf. Strauss 1991) and difficult to detect due to the incorporation of a third species (Davidson et al. 1984; Wootton 1992).

Those ecologists who agree that trophic interactions are important still debate whether primary control is by resources (bottom-up forces) or predators (top-down effects; Wiens 1989; Smith and Rotenberry 1990). According to the bottom-up view, organisms on each trophic level are regulated or limited by their resources (food limited). The top-down view holds that organisms are regulated or limited by predators (Power 1992). Hunter and Price (1992) offered a synthetic framework and sensible advice regarding this controversy. They suggested that ecologists not ask, "Do resource or predators regulate this particular population?" but rather, "What factors modulate resource limitation and predation in this system, determining when and where predation or resource will dominate in regulating populations?", and also suggested that relative roles of these ecological forces vary within the same system according to environmental heterogeneity.

The view of communities developed during 1960s and 1970s portrayed the stable and homogeneous world, in which none of spatial or temporal variations existed (cf. Wiens 1989). However, organisms are existing in a changing environment and themselves possessing a behavioral plasticity (Hunter and Price 1992). Moreover, these forces often influence organisms nonadditively (Faeth 1980; Schultz 1990). For example, Schultz (1990) revealed that phenolics, including tannins, which usually prevent the growth of lepidopterous larvae, facilitate the survival of the larvae under the presence of a kind of pathogen. A synthesis of top-down and bottom-up forces in communities will depend upon understanding of interactions between heterogeneous forces at all trophic levels (Karban 1989). Price (1986) emphasized that to understand the community-level phenomena, we should study the properties of its components and their interactions.

Community or food web structures in forest ecosystems are the most diverse and complex on the earth (Lawman and Nadkarni 1996). Various forms of life coexist, having interactions among them there. For example, insectivorous passerine birds intensely forage on herbivorous insects from various foraging microhabitats (Royama 1969; Remsen and Robinson 1990); herbivorous insects feed on plant tissues in various ways (Faeth 1980, Mole et al. 1988); and trees produce heterogeneous environments which birds and arthropods inhabit (Robinson and Holmes 1982). Dial and Roughgarden (1995) suggested effects of lizards on the structures of lower trophic levels by reducing the abundance of prey organisms and consequently the leaf damage. Lawton (1995) suggested that bird can be equivalent to the lizard in the forest canopy. On the other hand, a number of studies pointed out effects of prey distribution or microhabitat structure on bird foraging behaviors and community structures (Holmes and Schultz 1988, Parrish 1995). It was also shown that the abundance and quality of plants affect the distribution of herbivorous insects (Ohgushi and Sawada 1985, Schultz 1988). From these facts, we can expect

the close relationships between these components: birds would affect prey organisms and consequently plants, and inversely foraging behaviors of insectivorous birds would be affected directly by the distribution of herbivorous insects and indirectly by the quality of plant leaves. However, little is known about the interactions among three trophic levels involving birds, insects, and plants, in particular in forest ecosystems (Marquis 1996). The complexity of forest communities has been preventing us from close examination about the interactions among these trophic levels (Lawton 1995).

In this study, I focused on the heterogeneity in each component: diversity and versatility in bird foraging behaviors, temporal changes in distribution of herbivorous insects and their interspecific differences in method to avoid predators, and temporal and spatial differences in leaf quality (Fig. i).

I examined indirect effects of plant defenses on foraging behaviors of forest passerine birds via herbivorous insects, in particular lepidopterous larvae (Chapter I), assuming that decline in quality of deciduous tree leaves soon after the budbreak would cause seasonal changes in the distribution and abundance of herbivorous insects and eventually affect foraging behaviors of insectivorous birds.

Simultaneously, the reason why lepidopterous larvae changed their distribution at a particular season was examined by rearing experiments. Next, effects of the inverse direction, the top-down effects of insectivorous birds on the survival of leaf-rolling lepidopterous larvae and on forest canopy arthropods and plants were examined by field experiments (Chapter II).

To investigate these interactions, I adopted two methods: one was comparison of seasonal patterns among different components in the community, and the other was experimental manipulation of predators by exclosures or enclosures. The comparative studies will document the coincidental variations in the system, and the manipulative experiments can test hypotheses on causal factors responsible for such

variations (cf. Spiller and Schoener 1996). Some presumed pass-ways of interactions among components of a spring deciduous forest community are schematically shown in Fig. i.

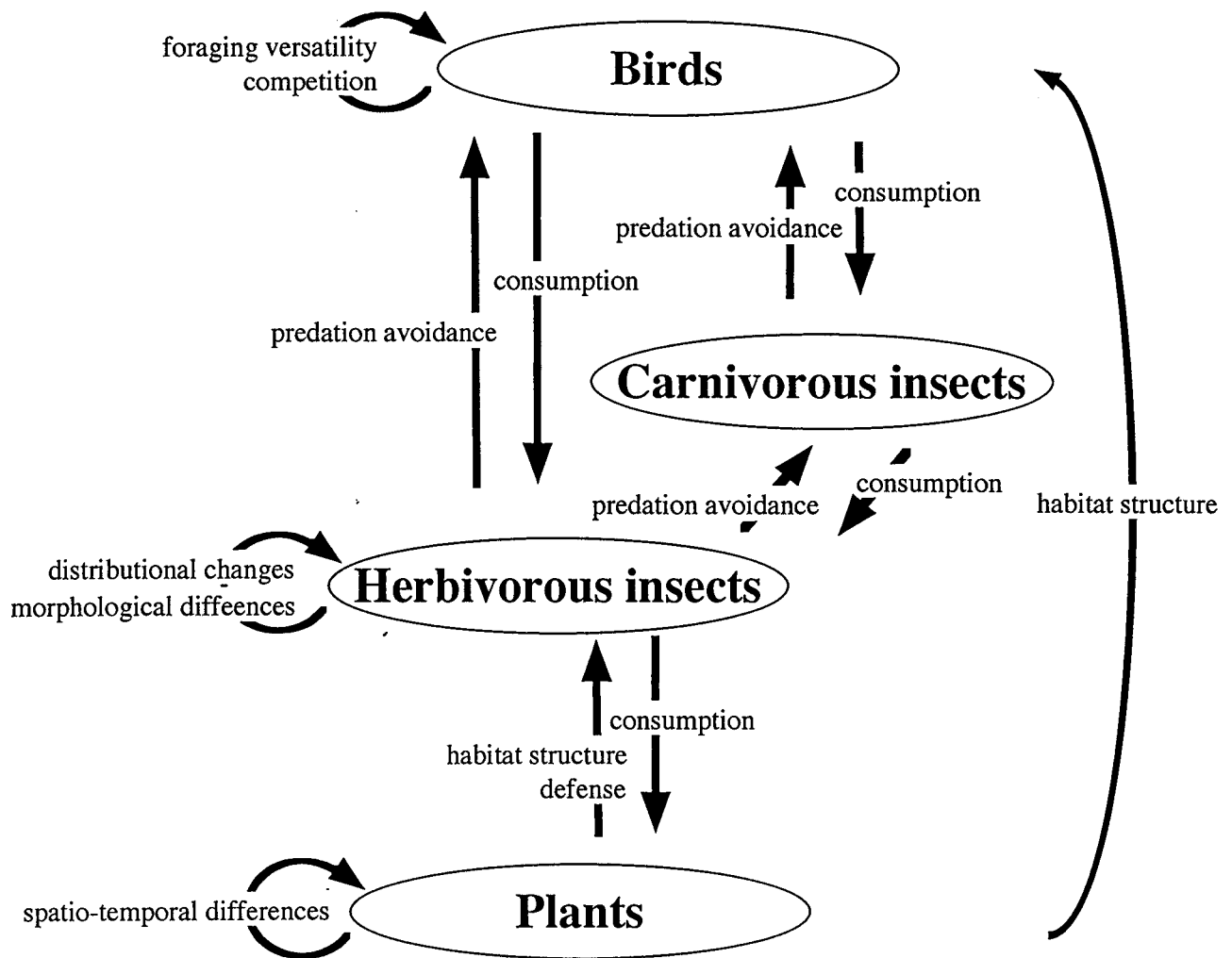


FIG. i. A hypothetical representation of interactions among some components of a spring deciduous forest community.

I

Seasonal changes in foraging behaviors of forest passerine birds:

Indirect effects of plant defense through herbivorous insects

Introduction

In temperate forests, leaves of many deciduous trees sprout almost simultaneously in spring (Kikuzawa 1983). Tree leaves rapidly change in quality and quantity, and develop various defenses against herbivorous insects (Feeny 1970, 1976; Rhoades and Cates 1976; Schweitzer 1979). The growth and survival of spring-feeding moth larvae are strongly affected by drastically changing leaf qualities such as toughness and nitrogen, water, and tannin contents soon after the budbreak (Feeny 1970; Schneider 1970; Schweitzer 1979; Raupp et al. 1988; Hunter 1991). According to Hunter (1991, 1993), the duration of spring foliage "window", the season when the leaf quality of host plant is most favorable, is quite short for moth larvae. Moreover, the leaf availability for herbivores varies spatially, among individuals of the same host plant species, and even within an individual plant (Raupp and Denno 1983). These findings imply that the timing of larval emergence has great influence on the subsequent growth and survival of spring-feeding lepidopterous larvae.

On the other hand, the distribution of arthropods, in particular herbivorous insects such as lepidopterous larvae, strongly influences the food availability for birds (Holmes and Schultz 1988). Bird foraging habitat should shift temporally in response to changes in distribution of prey to achieve higher breeding success (Lack 1971; Robinson and Holmes 1982; Wiens 1984; Greensberg 1987; Rosenberg 1993). A number of studies have revealed that the abundance and distribution of food

resources strongly affect foraging behaviors of birds (Lack 1954, Alatalo 1980, Holmes and Schultz 1988). Lack (1971) showed that there was clear-cut partitioning of foraging substrates in tree crowns among tit species. However, substrate selection and/or foraging maneuver is quite versatile and plastic according to the changes in the abundance and distribution of resources (Alatalo 1980, Moreno 1981). Most bird species require a larger amount of resources for feeding nestlings and fledglings in spring (Holmes et al. 1979). It is, therefore, expected in this season that insectivorous birds would change their foraging behaviors in response to changes in the abundance and distribution of arthropods. Holmes and Schultz (1988) suggested that bird species with different morphological and behavioral abilities to perceive and capture prey respond in different ways to the array of substrates, prey types, and prey abundances in a given forest. On the contrary, Hejl and Verner (1990) suggested that changes in foraging behavior and diet parallel among some species in the same habitat.

In this study, first I observed temporal changes in some characteristics of oak leaves and the abundance and distribution of arthropods within a forest in spring. Then, I examined the larval performance of *Conistra unimacula* (Noctuidae) in a rearing experiment, with special reference to effects of seasonal changes in quality of canopy and seedling leaves. Next, I examined the foraging behaviors of four forest bird species, great tit (*Parus major*), marsh tit (*Parus palustris*), narcissus flycatcher (*Ficedula narcissina*), and crowned willow warbler (*Phylloscopus occipitalis*), to reveal their responses to the changes in the abundance and distribution of arthropods within the forest.

Foraging behaviors of insectivorous birds are expected to be affected directly by the distribution of herbivorous insects and indirectly by the quality of tree leaves. Such tri-trophic interactions between birds, herbivorous insects, and plants can be

detected by focusing on phenological changes in performance of each component in this tri-trophic system with fine temporal resolution.

Methods

Study site

Field studies were performed in the Tomakomai Experimental Forest (TOEF) of Hokkaido University (42°40' N, 141°36' E). A study plot of 9 ha (300 x 300 m) was set up in a forest dominated by oak (*Quercus crispula*), maple (*Acer mono*), and linden (*Tilia japonica*). The canopy top was 15 to 25 m high, and saplings and current-year seedlings of the dominant tree species grew rather sparsely on the forest floor. Deciduous trees broke buds in mid May. Resident insectivorous birds, great tit and marsh tit, began to breed from mid May, and migrant birds, e.g. narcissus flycatcher and crowned willow warbler, from late May (cf. Ishigaki and Matsuoka 1972).

Measurements of leaf characteristics

Canopy oak trees sprouted their leaves in mid May, while the budbreak of current-year seedlings occurred about one month later in mid June. Every week from May 25 to June 22 and on July 7 and August 1, 1995, upper sun leaves at the top of the canopy were collected from an oak (25 m high) tree, located near the bird observation plot to measure leaf weight per shoot, leaf toughness, and water content. Tannin and nitrogen contents were measured every two weeks from May 25 to June 22 and on July 7 and August 1. Since current-year seedlings were quite sparse in 1995, I sampled seedling leaves once on July 7 about 3 weeks after their budbreak

under the crown of the tree of which canopy leaves were sampled for analyses of physical and chemical characteristics.

The total fresh weight of leaves was measured for each of 10 shoots, excluding all branches. The leaf toughness was measured for 10 leaves with a penetrometer (Feeny 1970). The water content was measured for 10 samples of approximately 5 g fresh leaves.

The tannin content per leaf dry weight was measured by the "hide powder method" (Japanese Society of Official Documents 1981): the amount of tannic substrates in the leaf extract was estimated by precipitating them with hide powder (collagen derived from animal skin). Four replicates of leaf samples were used for the measurement of tannin content. Tannic and non-tannic substrates were extracted from 3 g freeze-dried leaves with 60% (v/v) aqueous acetone. The extract was evaporated under vacuum to remove acetone. The residual solution was diluted with water to 100 ml in total volume. This solution was mixed with 2 g of hide powder which had been dried with a desiccant. The mixture was allowed to stand for 20 min. and then filtered. The hide powder remaining on the filter paper was dried again and weighed. The amount of tannin was estimated from the increased weight of the hide powder. The nitrogen content per leaf dry weight was measured with a C/N analyzer (C/N Coder, model MT1600: Yanaco Ltd., Tokyo, Japan). Ten samples of ca. 20 mg freeze-dried leaves were used for the measurement.

Insect sampling

To reveal seasonal changes in relative abundance and vertical distribution of arthropods, three different samplings were conducted in the forest around the bird observation plot. Arthropods in the canopy were collected by the beating method, and those on the forest floor were collected by sweeping. Lepidopterous larvae spinning down from the canopy to the floor were caught by sheet traps.

Beating samplings were made on oak trees at weekly intervals from May 23 to June 20 and on July 10 and 30, 1995. Climbing a tree (10-25 m high) by the method of Perry (1978), I repeatedly beat branches, and arthropods which dropped onto a tray (80 x 80 cm) under the branches were collected. This was randomly replicated ten times for different parts of a single tree. The same tree was never sampled twice or more to avoid effects of previous samplings. Leaf-mining and leaf-rolling arthropods, which were rarely collected by this method, were excluded from the analysis.

To assess the abundance of lepidopterous larvae spinning down from the canopy, two sheet traps (5 x 4 m: a sheet coated with tanglefoot (Fuji Ltd, Tokyo, Japan) along the periphery to prevent escape) were set ca. 0.5 m above the floor under the canopy dominated by oak trees. Each trap was inspected three times per day on June 1, every other day during the period from June 5 to 25, and on June 29 and July 3.

Arthropods on the forest floor were collected by sweeping once a week from June 1 to 26 and on July 4 and 12. At each sampling, an area 400 m² square was swept with an insect net (40 cm in diameter) for 30 min. The same area was sampled only once during the study period.

Collected arthropods were classified into two categories, lepidopterous larvae and other arthropods. They were dried at 60°C for 24 h and then weighed to the nearest 0.1 mg. Lepidopterous larvae were identified to the species level, and the number of individuals was counted separately for each of three developmental stages (the first and second instars, the third to fifth instars, and the last instar; cf. Yoshida 1985).

Rearing experiment

In order to compare the performance of lepidopterous larvae fed on oak leaves of different qualities, larvae of *C. unimacula* (Noctuid), which is a representative of the spring-feeding species on oak trees (see. Appendix), were reared on canopy leaves and on current-year seedling leaves. Eggs were obtained on March 24 from females collected on March 23, 1995, by syrup traps set on trunks of oak trees in TOEF. Of the 18 species collected, *C. unimacula* was the dominant species, accounting for 49% of the total individuals. Most of the females laid eggs immediately in the laboratory. One hundred eggs were sampled from five females (20 eggs from each female). These eggs were stored outdoors. All the eggs hatched on May 29, 10 days after the budbreak of the oak trees, from which leaves were taken for food and for measurement of leaf characteristics. Each individual was reared alone under the outdoor temperature and was supplied with a 5 × 3 cm piece of fresh leaf every day. Twenty larvae from each female were divided into two groups. One group (fifty individuals in total) was reared on canopy leaves throughout the experiment period. The other group (fifty individuals) was also reared on canopy leaves until June 14; *C. unimacula* larvae usually spin down from the canopy in mid June (Murakami personal observation). Thereafter, the larvae were reared on seedling leaves, which sprouted in early to mid June. Experimental individuals began to molt into the 5th instar at this time. The duration of each instar for each individual and the number of surviving individuals for each brood were recorded.

Bird foraging behaviors

Individuals of four dominant species, great tit, marsh tit, narcissus flycatcher, and crowned willow warbler, were identified by color rings, and their foraging behaviors were observed for five consecutive days per week during the breeding season from May 24 to July 5, 1995. A 20-m square grid was set up on the forest floor by spacing

color markers. I walked about on the systematic basis (cf. Kendeigh 1944) in the study plot between 5:00-11:00 am. When a foraging individual was encountered, it was followed as long as possible. Whenever the bird made a foraging maneuver, the height at which they foraged (foraging height), the prey type (lepidopterous larvae or other arthropods), the kind of attack (sallying, gleaning, or pecking (unfastening leaf rolls, leaf galls, or barks)), and the substrate (air, leaf, twig, or trunk) were recorded (cf. Holmes et al. 1979). Foraging heights were estimated to the nearest 2 m. An individual previously observed on the same day was left out so as to avoid the bias due to a particular individual. The kinds of attacks and substrates were combined as foraging methods and classified into 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 percentage of lepidopterous larvae in prey and that of each foraging method were calculated for each day. The data were summed for each week in the survey period. In consequence, the overall study period was divided into six intervals: P (Period) 1, May 24 - 30; P2, May 31 - June 6; P3, June 7 -13; P4, June 14 - 20; P5, June 21 - 27; P6, June 28 - July 4.

Statistical Analyses

Leaf characteristics The Kruskal-Wallis test was used to reveal phenological changes in characteristics of canopy leaves and a post hoc test by Scheffe's F was carried out when significant differences were encountered. The total fresh weight, the toughness, the water content, and the nitrogen content were compared between canopy and seedling leaves collected on July 7 by a one-way ANOVA, but the tannin content by the Mann-Whitney U test.

Arthropod distribution A two-way ANOVA (factor = sampling period, arthropod category) was used to reveal the seasonal changes in the relative abundances of

lepidopterous larvae and other arthropods in the canopy, and a post hoc test by Fisher's PLSD was carried out when significant differences were encountered.

Rearing experiment A two-way ANOVA (factor = treatment, brood) was used on the larval duration of each individual to reveal the differences in the larval period between the treatments and among the broods. Statistical tests were invalid on the larval duration in the 5th and last instars because heavy mortality occurred in the rearing on canopy leaves. Wilcoxon matched-pairs signed-ranks tests were adopted to reveal the differences in the number of survivors at the 5th and last instars.

Bird foraging behavior A two-way ANOVA (factor = season, species) was used to reveal the seasonal and interspecific differences in the foraging height and the proportion of lepidopterous larvae in prey. Furthermore, the seasonal and interspecific difference in foraging methods was analysed by a two-way MANOVA (factor = season, species).

Percentage data were arc-sin transformed for normalization. All statistical tests were two-tailed. In all cases, statistical significance was evaluated at $P < 0.05$.

Results

Leaf characteristics

The leaf weight per shoot in the canopy significantly increased from the budbreak to early June, and attained a plateau thereafter (Kruskal-Wallis test; $df = 6$, $P < 0.001$; see Fig. 1-1a for the result of post hoc test by Scheffe's F). Seasonal changes in the

leaf toughness proceeded nearly in parallel with those in the leaf weight per shoot. Leaves significantly increased their toughness after emergence and attained a plateau by early June ($df = 6$, $P < 0.001$; Fig. 1-1b). The water content per fresh weight of leaf was high from the budbreak to early June, but thereafter significantly decreased and attained a constant level from mid June ($df = 6$, $P < 0.001$; Fig. 1-1c). The tannin content per leaf dry weight significantly increased during the study period ($df = 4$, $P < 0.05$; Fig. 1-1d). The nitrogen content per leaf dry weight significantly decreased to less than half of the initial level in mid June ($df = 4$, $P < 0.01$; Fig. 1-1e).

Seedling leaves differed significantly in quality from canopy leaves on July 7, being softer, fresher, more nutritious, and lower in the tannin content than canopy leaves (Table 1).

Arthropod abundance and distribution

To reveal seasonal changes in the abundance of arthropods in the canopy, the biomasses were compared between lepidopterous larvae and other arthropods over the study period. A two-way ANOVA revealed significant effects of the sampling period and the arthropod category (period, $F = 11.45$, $df = 6, 126$, $P < 0.001$; category, $F = 23.09$, $df = 1, 126$, $P < 0.001$; Fig. 1-2a). Interaction effect was also significant ($F = 7.55$, $df = 6, 126$, $P < 0.001$). The biomass of lepidopterous larvae was conspicuously large from late May to mid June in the oak canopy, but rapidly declined thereafter and remained at a low level from late June. Lepidopterous larvae was significantly more abundant than that of other arthropods from early June to mid June. Complementarily, spinning down of lepidopterous larvae from the canopy began from early June, reached a conspicuous peak in mid June, and then decreased rapidly (Fig. 1-2b). Due to this downward migration, lepidopterous larvae on the forest floor increased their biomass from early June, reached a peak in mid June, then

gradually decreased and reached a low level in early July (Fig. 1-2c). However, the peak in early June was caused by individuals of *Spilosoma inaequalis*, which overwintered at the larval stage on the ground. The abundance of other arthropods remained at low levels throughout the study period both in the oak canopy and on the forest floor.

In the samples of lepidopterous larvae collected from the canopy, sheet traps, and floor, *Inurois fumosa* was the most dominant (24% of the total number of lepidopterous larvae), followed by *Cosmia exigua* (11%), and *Telorta edentata* (9%) (cf. Appendix). The other Lepidoptera species each accounted for less than 4%. The seasonal life histories, especially at the larval stage, of the three predominant species within the forest can be sketched out by combining the data from the canopy, by the sheet traps, and on the forest floor. In Fig. 1-3, seasonal changes in the number of collected individuals and the age structure of larval populations sampled by the three methods are shown for each species. Canopy populations of the three species showed peaks in late May to early June and mostly consisted of the 1st and 2nd (white in Fig. 1-3) or the 3rd to 5th (gray) instars. A small number of the last instars were collected from the oak canopy for *I. fumosa* from early to mid June but none for *C. exigua* and *T. edentata*. Spinning down from the canopy occurred mostly in mid June in the three species. The spinning-down populations included larvae not only of the last instar but also of young instars. The mid-June conspicuous peak in the spinning-down population of *I. fumosa* mostly consisted of full-grown larvae at the prepupal stage. On the forest floor, young larvae of the three species were collected from early June and reached a peak in mid June, and the last instar larvae of *C. exigua* and *T. edentata* appeared from mid June to early July. However, practically no last instar larvae of *I. fumosa* were collected on the forest floor.

Larval performance in the rearing experiment

From the 1st-2nd to the 4th instars, no mortalities occurred in either group reared on canopy leaves or on canopy/seedling leaves. No significant effect of the treatment or brood was observed in the duration of each instar (Two-way ANOVA; the 1st-2nd instar, treatment, $F = 1.73$, $df = 1$, 90, $P = 0.192$; brood, $F = 0.026$, $df = 4$, 90, $P = 0.999$; the 3rd instar, treatment, $F = 0.529$, $df = 1$, 90, $P = 0.469$; brood, $F = 0.864$, $df = 4$, 90, $P = 0.489$; the 4th instar, treatment, $F = 0.604$, $df = 1$, 90, $P = 0.439$; brood, $F = 0.321$, $df = 4$, 90, $P = 0.863$; Table 2), with interaction being insignificant (the 1st-2nd instar, $F = 0.130$, $df = 4$, 90, $P = 0.971$; the 3rd instar, $F = 0.475$, $df = 4$, 90, $P = 0.754$; the 4th instar, $F = 0.274$, $df = 4$, 90, $P = 0.894$). At the 5th and last instars, the numbers of surviving individuals were significantly larger in the canopy/seedling group than in the canopy group (Wilcoxon test; the 5th instar, $P < 0.05$; the last instar, $P < 0.05$, Table 2). Heavy mortality (90%) arose at the 5th instar stage after mid June and all of the larvae died out at the last instar, when they were continuously fed on canopy leaves. When the food material was changed from canopy leaves to seedling leaves after mid June (at the end of the 4th instar stage), however, 72% of the larvae survived at the 5th instar stage, and 30% succeeded to pupate.

Bird foraging behaviors

In the study plot, 11 individuals of great tit, 16 of marsh tit, 21 of narcissus flycatcher, and 19 of crowned willow warbler were recorded.

Foraging height The foraging height significantly varied seasonally ($F = 6.470$, $df = 6$, 1573, $P < 0.001$; Fig. 1-4) and among bird species ($F = 137.02$, $df = 3$, 1573, $P < 0.001$) with significant interaction ($F = 7.948$, $df = 18$, 1573, $P < 0.001$). Great tits, marsh tits, and the warblers continued to forage in the canopy throughout the study

period, whereas the flycatchers changed their foraging height: they foraged in the canopy from late May to mid June, then on the forest floor in late June, and again in the canopy from early July.

Prey type I could identify the prey type in 68% of the total foraging maneuvers observed. The prey type significantly varied seasonally ($F = 64.96$, $df = 5$, 96 , $P < 0.001$; Fig. 1-5) and among bird species ($F = 5.647$, $df = 3$, 96 , $P < 0.0013$) with significant interaction ($F = 4.371$, $df = 15$, 96 , $P < 0.001$). From late May to mid June, all the bird species mostly foraged on lepidopterous larvae. In late June, the flycatcher continued to forage on lepidopterous larvae, whereas the other bird species reduced the utilization ratio of lepidopterous larvae. Then in July, all the bird species utilized lepidopterous larvae at the ratio of ca. 60%.

Foraging method The foraging methods significantly differed both among bird species and across the seasonal periods (MANOVA; Hotelling-Lawley Trace: bird species, value = 12.77, $df = 21$, $F = 53.94$, $P < 0.001$; Period, value = 1.669, $df = 35$, $F = 2.176$, $P < 0.001$; Fig. 1-6) with significant interaction (value = 1.667, $df = 105$, $F = 1.404$, $P = 0.008$). The flycatcher mostly foraged by Sally from leaves throughout the study period (more than 60% of the total foraging maneuvers) and rarely utilized twigs and trunks (less than 15%). The other species, great tit, marsh tit, and the warbler, frequently foraged by Glean from leaves. Great tit also utilized Pecking on leaf rollers, and marsh tit Pecking on twigs and trunks. From late June to July, these three species came to forage more frequently from twigs and trunks (ca. 40%) than the previous period (ca. 20%).

Discussion

Interactions between plants and herbivores

The quality of oak canopy leaves changed dramatically during about one month after the budbreak. The leaves were soft, rich in the water and nitrogen contents, but low in the tannin content until early June, whereas they became tough, poor in the water and nitrogen contents, but high in the tannin content after mid June. A number of studies have demonstrated the ephemerality of spring foliage as a high quality food resource for herbivorous insects: only for a short period after the budbreak, young leaves facilitate the growth and the survival of herbivorous insects more than old leaves (e.g. Feeny 1970; Kraft and Denno 1982; Stamp and Bowers 1990; Hunter 1993). Mattson (1980) pointed out the importance of nitrogen as a limiting resource for lepidopterous larvae, and Scriber (1977) demonstrated a synergistic effect of water and nitrogen contents. Digestibility-reducing defenses of leaves (e.g. tannin or toughness) also affect the fitness of herbivores (Feeny 1970; Karowe 1989), although some contrary evidence has been reported (Bernays et al. 1989; Hunter and Schultz 1993). To increase their survival, spring-feeding lepidopterous larvae should completely synchronize their larval growth period with the "window" of spring foliage, the time when the leaf quality of host plants is most favorable (cf. Schneider 1980; Hunter 1993). Too early hatching before leaf emergence causes the serious mortality on the larvae by starvation, whereas hatching too late is detrimental because of the decline in leaf quality of canopy foliage. In this study, the biomass of lepidopterous larvae was large from late May to mid June in the oak canopy, but thereafter rapidly decreased.

In mid June, a number of lepidopterous larvae, which spun down from the canopy to the floor, were collected by sheet traps. In temperate deciduous forests, the migration of lepidopterous larvae from the canopy to the forest floor was

regarded as for pupation (Feeny 1970; Yoshida 1985). In this study, the larvae of *I. fumosa* spun down to the floor mostly at the full-grown stage (69% of the total larvae collected by sheet traps), and disappeared quickly on the forest floor (Fig. 1-3). They appeared to synchronize their larval growth period with the "window" of spring foliage, and as a result, completed their growth in the canopy and pupated on the forest floor immediately after spinning down from the canopy. In contrast, the larvae of other two species, *C. exigua* and *T. edentata*, spinning down from the canopy, consisted of not only full-grown individuals (54% of the total larvae in *C. exigua*, 27% in *T. edentata*) but also many immatures, which suggests that they failed to complete their growth in the canopy by this time. The timing of budbreak varies to some extent from year to year (Hunter and Lechowicz 1992; Cushman et al. 1994), from species to species (Hunter and Lechowicz 1992), and even among individual trees of the same species within the same region (Schneider 1980; Hunter 1993). This unpredictability of the budbreak may make it difficult for insects to completely synchronize their emergence with the phenological "window". The larvae that can not complete their growth before the end of the "window" in the canopy foliage probably migrate from the canopy at the immature stages.

On the forest floor, a considerable number of lepidopterous larvae, which had spun down from the canopy, were observed feeding on seedlings of canopy tree species (Murakami, personal observation). The rearing experiment showed that the decline in quality of canopy leaves seriously decreased the survivorship of lepidopterous larvae, and that hatching about ten days after the budbreak was fatal for them. All of the larvae which were continuously fed on canopy leaves died in mid June. This result was almost concurrent with the migration pattern of many lepidopterous larvae in the forest. Although Feeny (1970) stated that most of the migrant larvae failed to complete their growth on the ground, my results suggest that some of them succeed to pupate if an alternative food resource is available on the

forest floor. Seedling leaves are considered to be less resistant to herbivory, having a lower tannin content. Under the light-limited condition on the forest floor, the carbon gain by tree seedlings from photosynthesis may be insufficient, which causes the low C/N ratio in seedling leaves (Harrington et al. 1989). The shortage of carbon gain probably compels seedlings to produce less secondary chemical matter such as tannins and results in less defensive leaves (cf. Herms and Mattson 1992). In addition, the leaves of oak seedlings emerge in early to mid June. These phenological, physical, and chemical characteristics of oak seedling leaves may make them good food resources for lepidopterous larvae migrating from the canopy.

It is well known that oak trees perform mast seeding (Sork 1993). Accordingly, many seedlings would be established under the crowns of oak trees in a given year, but no or very few seedlings would be established in other years. This fluctuation in the amount of seedlings due to mast seeding must greatly affect the survival of spring-feeding lepidopterous larvae on the forest floor.

The patterns of seasonal changes in the abundance and distribution of other arthropods differed from that of lepidopterous larvae; they remained at low levels throughout the study period. Because a number of the other arthropods in my samples were not herbivores, their life cycles probably were not affected by the strengthening of leaf defenses.

Interactions between birds and herbivores

The flycatcher foraged in the canopy from late May to mid June but on the forest floor in late June. The foraging habitat shift of the flycatcher from the canopy to the floor was nearly synchronous with the decline in biomass of lepidopterous larvae in the canopy, but a little later than the peak of larval abundance on the forest floor. This implies that the foraging habitat shift by the flycatchers was probably the result of the decline in the abundance of lepidopterous larvae in the canopy rather than the

increase on the floor. The other bird species, however, continued to forage in the canopy even after this critical moment. Several studies suggested that seasonal trends in the foraging behavior and diet are parallel among different bird species in the same habitat (Alatalo 1980; Rotenberry and Wiens 1980; Hejl and Verner 1990). Smith et al. (1978), however, showed that such parallel responses of co-existing species are dependent on the amount of food resources: under resource-limited conditions co-existing species separate their foraging habitats from each other. In this study, the flycatcher foraged more frequently on lepidopterous larvae than the other bird species in late June, when the abundance of the larvae was decreased in the canopy. On the other hand, crowned willow warbler and great and marsh tits foraged more frequently on other arthropods, especially from late June to July. Thus, different bird species coped with the abrupt decrease of the most important food resource (lepidopterous larvae) in the canopy in mid June by different responses: the flycatcher changed its foraging habitat from the canopy to the floor, but the other species came to forage more frequently on other arthropods from twigs or trunks in the canopy than before.

These different responses may correspond to their species-specific foraging tactics. Rosenberg (1993) suggested that foraging tactics used by birds considerably affect the accessibility toward prey organisms on different substrates. Holmes and Recher (1986) and Robinson and Holmes (1982) also suggested that the difference in foraging method affects the prey-type selection and that gleaner species can obtain smaller prey than sallyer species. In this study, the flycatcher foraged mainly by Sally, whereas the other species frequently used Glean or Peck. The flycatcher (sallyer) was probably faced with difficulty to find alternative food resources in the canopy in mid to late June when lepidopterous larvae, which are larger than other arthropods within the forest (Murakami, unpublished), disappeared from the canopy, and thus changed its foraging habitat, following lepidopterous larvae having

migrated from the canopy to the forest floor. The other species, however, did not change their foraging habitats in this season but began to prey more frequently on other arthropod as alternative resources than before. Alternative foraging substrates, twigs and trunks, also became to be utilized by these species from late June. In early July, the flycatcher resumed to forage in the canopy. When the density of lepidopterous larvae decreased both in the canopy and on the floor, the flycatcher probably foraged more efficiently in the canopy than on the floor due to its innate foraging behavior (Wiens 1984, Murakami, in submit.). Foraging heights differed among the studied bird species even within the canopy layer: the two tit species foraged in higher canopies than the flycatcher and the warbler (Fig. 1-4). Hutto (1981) suggested that each bird species is adapted to forage most effectively in a particular microenvironment, which occurs at a different height in foliage. On the other hand, Alatalo et al. (1987) showed that experimental removal of a tit species resulted in the shift of foraging microhabitat in the other tit species, suggesting the presence of interspecific competition among bird species. Interspecific competition should be taken into account for further understanding of the versatility of bird foraging behaviors.

Habitat segregation and resource partitioning are of primary importance for co-existence of different species in bird communities (MacArthur 1958; Lack 1971; Schoener 1974). Robinson and Holmes (1982) suggested that foraging behaviors of birds, vegetation structure, and distribution pattern of resources interact to provide opportunities in such ways that birds can successfully search for and capture prey. Therefore, the spatio-temporal variation in resource distribution would considerably affect the foraging behaviors of birds, and hence bird communities (Wiens 1989, Maurer 1990). This study documented species-specific responses of different bird species to the spatio-temporal variation in resource abundance and distribution. Further investigation on relations between such versatile foraging behaviors of birds

and fluctuation of resource abundance and distribution will provide a deeper insight into the mechanisms for species co-existence in bird communities (cf. Smith and Rotenberry 1990).

Tri-trophic interactions

Many studies have demonstrated that various defense traits of plants affect the survival and the growth of herbivorous insects (Feeny 1970; Rhoades and Cates 1976; Raupp and Denno 1983; etc.), and that changes in arthropod distribution cause shift in bird foraging behaviors (Greensberg 1987; Raley and Anderson 1990; Rosenberg 1993). However, connecting these two phenomena, only few studies have dealt with interactions between three trophic levels (e.g., Fawler et al. 1991; Marquis and Wheran 1994). This study provides evidence for the tri-trophic interactions.

The strengthening defense traits of oak canopy leaves forced almost all lepidopterous larvae to migrate from the canopy to the forest floor in mid June. Of the migrants, immatures having failed to complete larval growth during the “window” of spring foliage spun down to seek alternative food resource on the forest floor. They were observed feeding on seedling leaves, the quality of which was still good at that moment, in the understory of their host canopy trees. *Narcissus* flycatchers came to forage on such lepidopterous larvae on the forest floor in late June, whereas other insectivorous birds shifted their diets from lepidopterous larvae to other arthropods and foraging substrates from leaves to twigs or trunks in the canopy. Thus, foraging behaviors of insectivorous birds were indirectly affected by plants through herbivorous insects.

Table 1. Differences in five characteristics (mean $\pm$ SE) between canopy and seedling leaves.

Leaf characteristics		Canopy	Seedling	One-way ANOVA	
				<i>F</i>	<i>P</i>
Leaf weight (g/shoot)	<i>n</i> =10	4.2 $\pm$ 0.4	0.25 $\pm$ 0.02	370.4	< 0.001
Leaf toughness (g)	<i>n</i> =10	332 $\pm$ 22	154 $\pm$ 9.8	49.99	< 0.001
Water content (% wet weight)	<i>n</i> =10	51.1 $\pm$ 0.01	70.0 $\pm$ 0.01	113.5	< 0.001
Nitrogen content (% dry weight)	<i>n</i> =10	1.74 $\pm$ 0.15	6.1 $\pm$ 0.13	1272	< 0.001
Tannin content (% dry weight)	<i>n</i> =4	1.16 $\pm$ 0.01	0.65 $\pm$ 0.005	16*	< 0.021

* Mann-Whitney U-value

Table 2. Duration and number of survival individuals (means $\pm$ SE) at each growth stage in two group of *Conistra unimacula* larvae, of which was continuously fed on canopy leaves of *Quercus crispula* and the other of which was first fed on canopy leaves and then on seedling leaves after the 5th instar. Means and SE for the number of surviving individuals were calculated for each of five larval broods served to the experiment.

Growth stage	Canopy Group		Canopy / Seedling Group	
	Duration (days)	Number of surviving individuals	Duration (days)	Number of surviving individuals
1st-2nd instar	10.0 $\pm$ 0.2	10	9.8 $\pm$ 0.2	10
3rd instar	4.3 $\pm$ 0.4	10	4.2 $\pm$ 0.2	10
4th instar	5.0 $\pm$ 0.3	10	5.2 $\pm$ 0.3	10
5th instar	10.0 $\pm$ 0.2	1.0 $\pm$ 0.4	10.0 $\pm$ 0.6	7.2 $\pm$ 0.4
Mature instar	-----	0	14.8 $\pm$ 0.7	3.0 $\pm$ 0.3

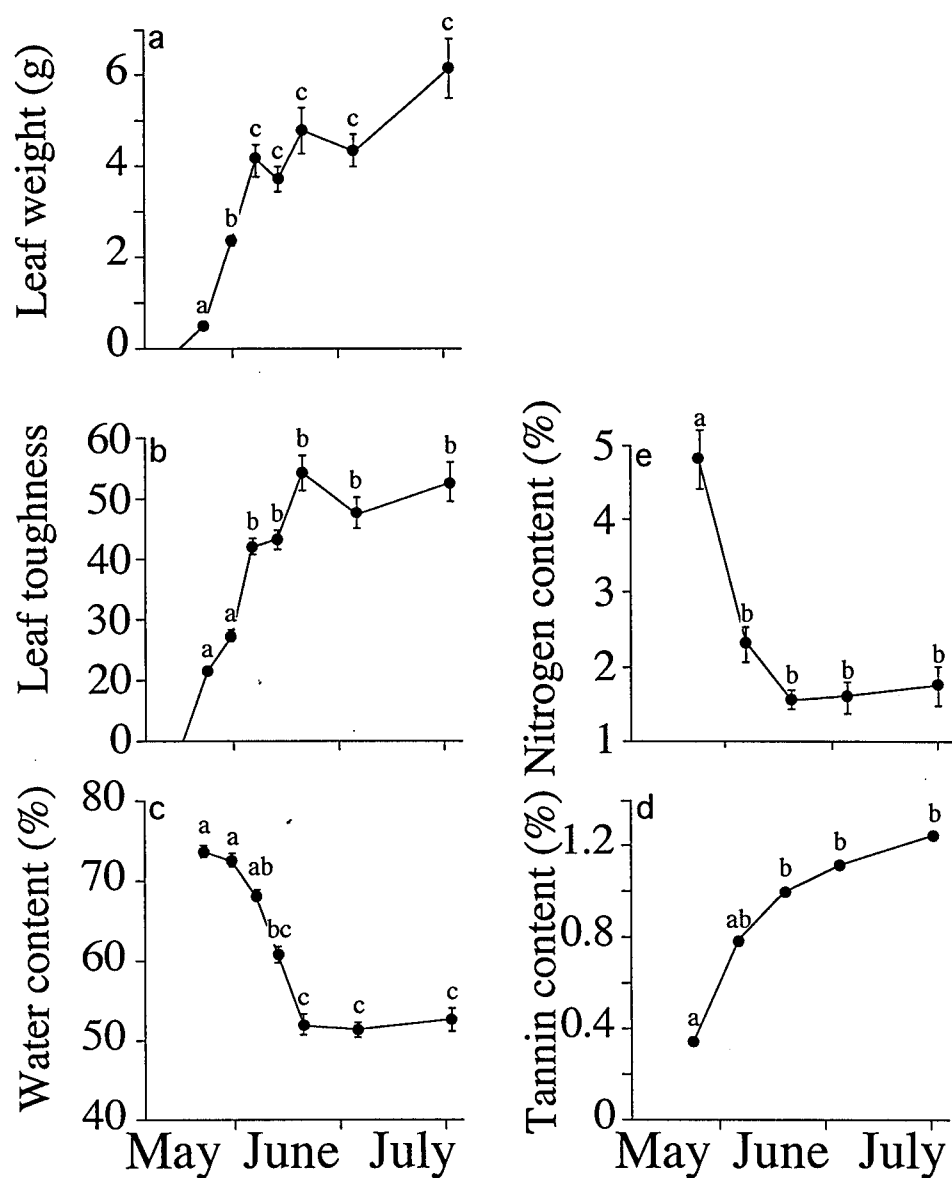


FIG. 1-1. Seasonal changes in qualities of oak leaves, after the budbreak: (a) fresh weight of leaves per shoot, (b) leaf toughness, (c) water content per fresh leaf weight, (d) nitrogen content per dry leaf weight, and (e) tannin content per dry leaf weight.

Error bars are standard errors of the means.

Letters above vertical lines indicate the results of multiple comparison test (Scheffe's F , $P < 0.05$); the same letters indicate nonsignificant differences.

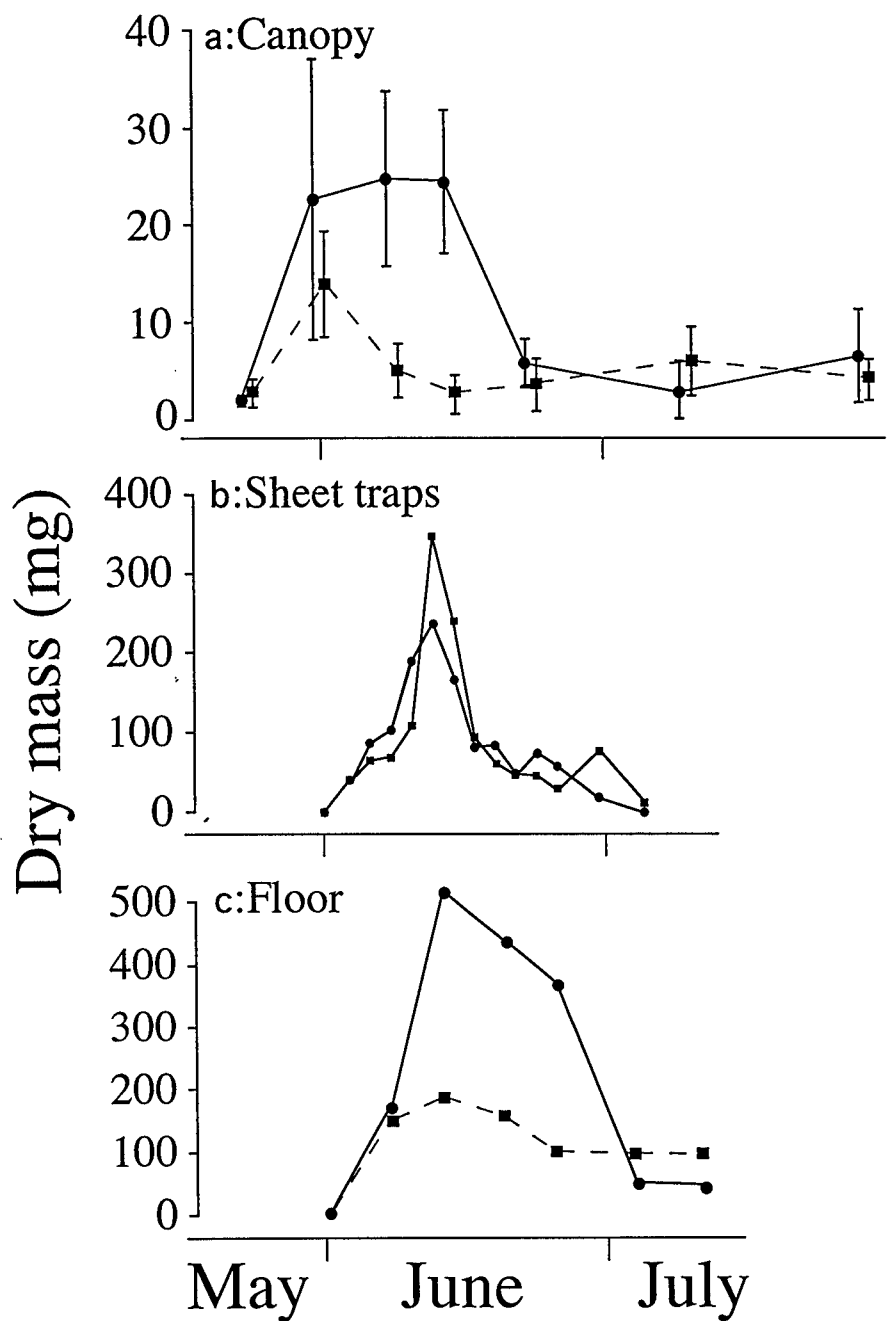


FIG. 1-2. Seasonal changes in biomass (dry weight) of arthropods collected (a) from the canopy, (b) by sheet traps, and (c) on the floor. Solid lines indicate lepidopterous larvae and broken lines other arthropods. The results of sheet trapping are shown separately for each of two traps. Error bars are 95% confidence intervals of the means.

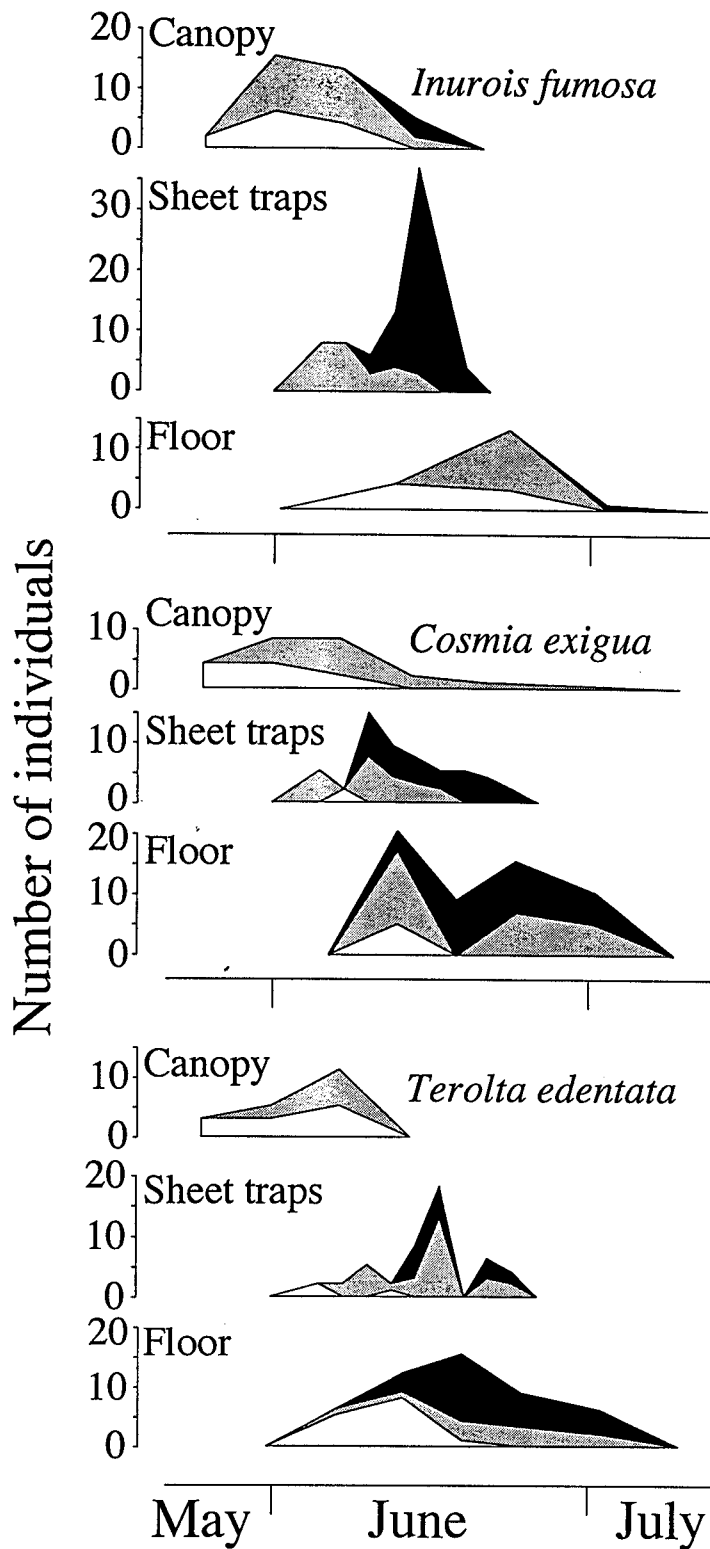


FIG. 1-3. Seasonal trends of larval populations in three most predominant lepidoptera species sampled from the canopy, by sheet traps, and on the forest floor, with indication of the age structure (□ the 1st and 2nd instars, ▨ the 3rd to 5th instars, and ■ the last instar).

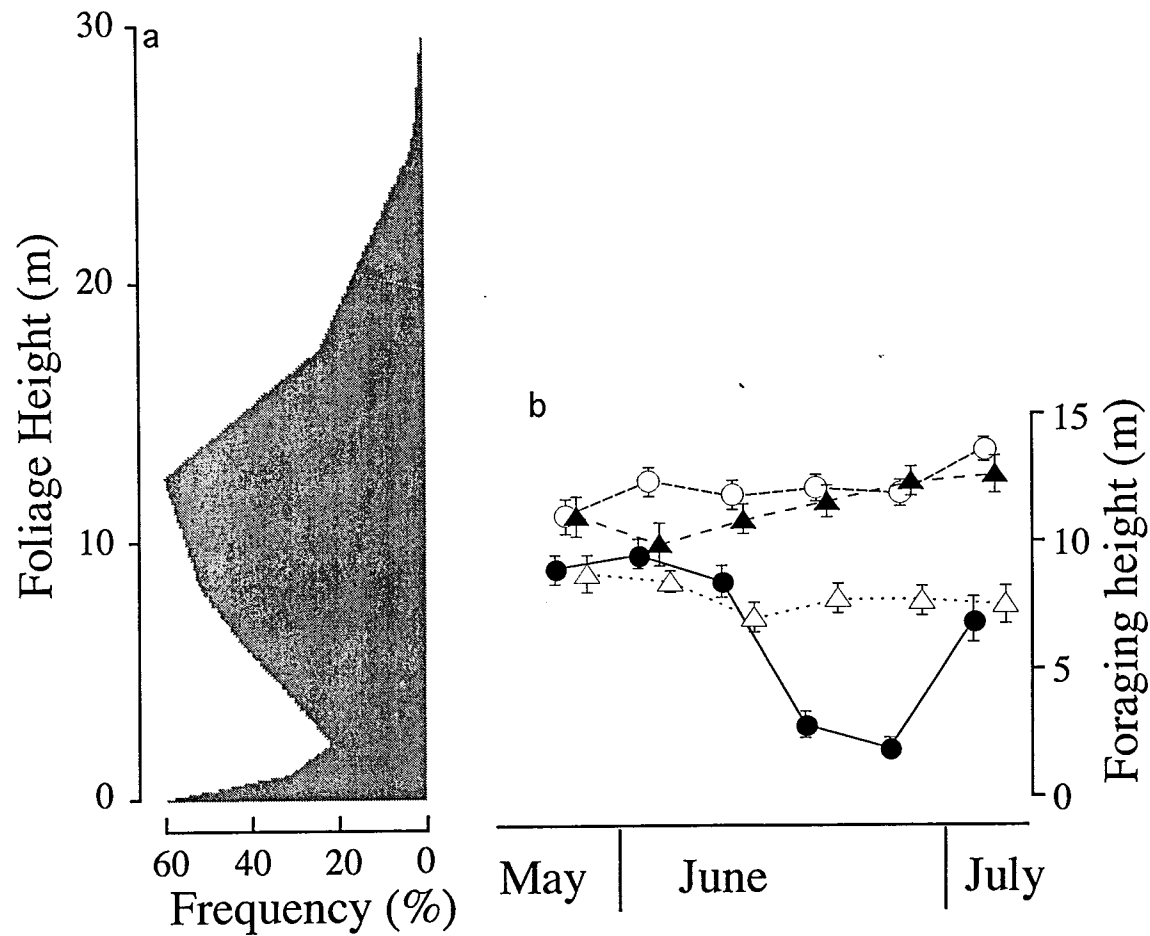


FIG. 1-4. Vertical foliage distribution in the study plot (a) and seasonal changes in the foraging heights of four bird species: narcissus flycatcher (●), great tit (○), marsh tit (▲), and crowned willow warbler (△) (b). Error bars are standard errors.

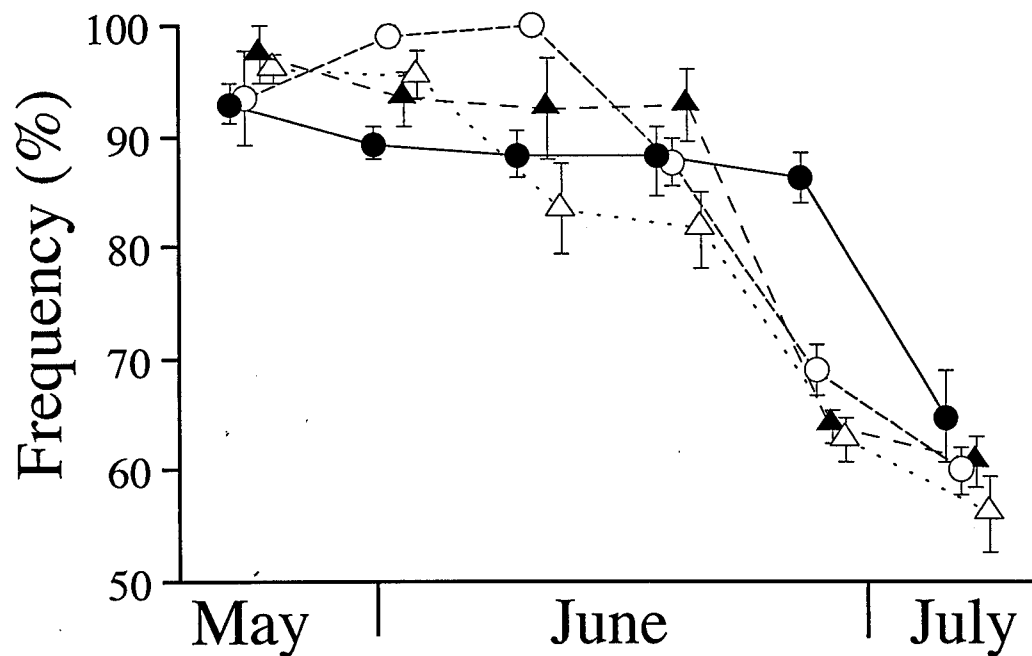


FIG. 1-5. Seasonal changes in the proportion of lepidopterous larvae preyed by four bird species: narcissus flycatcher (●), great tit (○), marsh tit (▲), and crowned willow warbler (Δ). Error bars are standard errors.

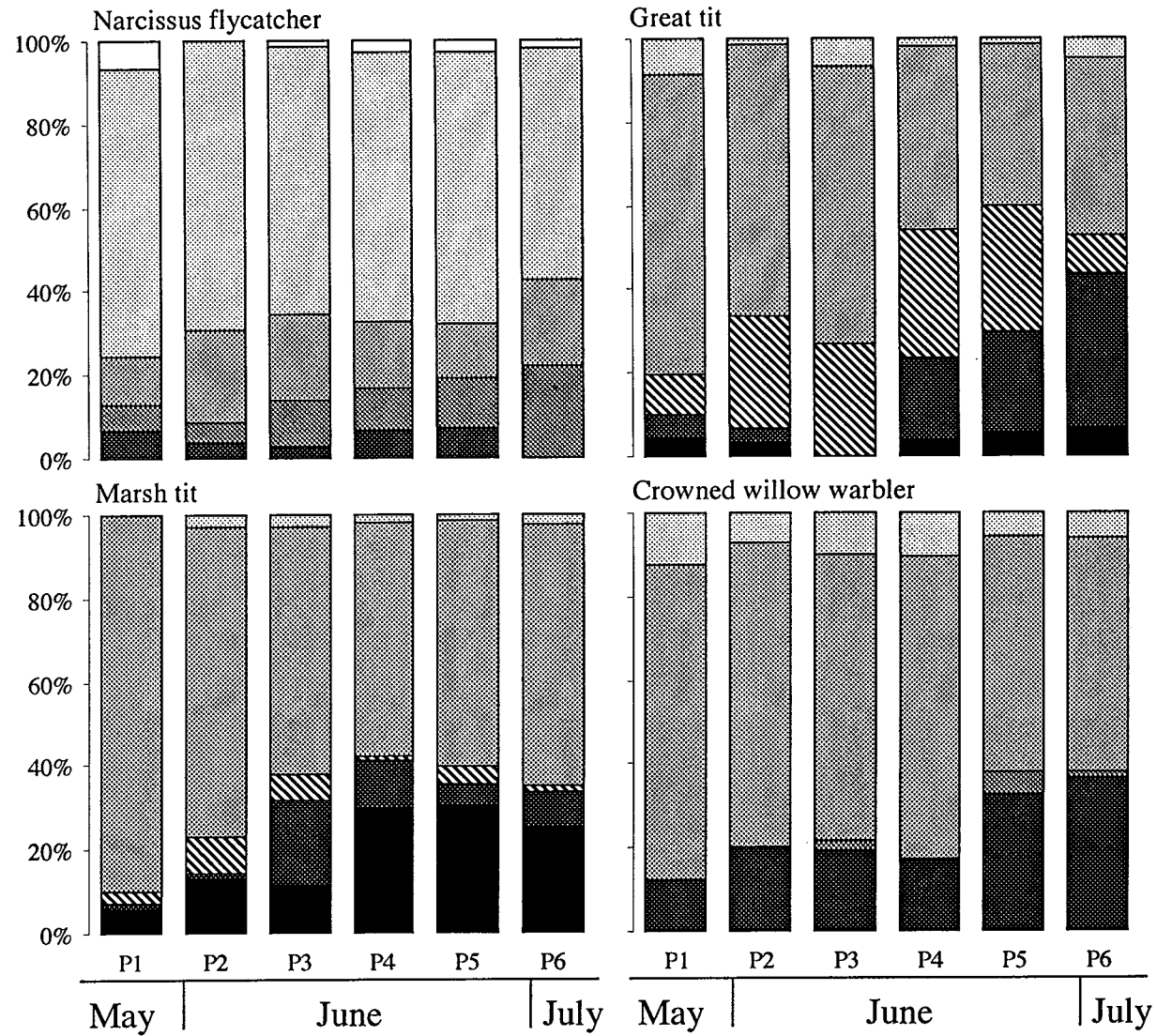


FIG. 1-6. Seasonal changes in the foraging methods employed by four bird species: Air Sally, Leaf Sally, Leaf Glean, Leaf Peck, Twig and Trunk Sally, Twig and Trunk Glean, and Twig and Trunk Peck.

II

Roles of insectivorous birds in forest ecosystems:

Experimental approaches

In the previous chapter, the bottom-up effects from plants to birds via herbivorous insects were shown by the coincidence of some seasonal events among them. In this chapter, effects in the inverse direction from birds to insects and further to plants are examined using experimental methods. A well-designed experimental manipulation is the *sine quo non* for determining the importance of interactions among different trophic levels (Spiller and Schoener 1990b, Wootton 1994). A number of experiments with enclosures or exclosures quantified effects of predators on lower trophic levels in grassland (Wiens 1973, Joern 1986, Bock et al. 1992), intertidal (Paine 1988, Menge 1991, Wootton 1992, 1993), freshwater (Carpenter et al. 1985, Power 1990), or mangrove (Spiller and Schoener 1990b) systems. However, experimental manipulations are troublesome in structurally complex ecosystems such as forests (cf. Holmes and Schultz 1988; Schoener 1988; Lawton 1995). In this chapter, first I examine effects of avian predation on leaf-rolling lepidopterous larvae using exclosures. Next, I quantify effects of two insectivorous bird species on lower trophic levels by manipulating the presence and absence of birds within forest canopy enclosures. Most of experimental studies so far conducted in forest ecosystems manipulated only a portion of forest (Holmes et al. 1979, Atlegrim 1989, Gunnarsson 1996, Marquis and Whelan 1994). Crawford and Jennings (1989) mentioned that “it was impractical and unsafe to install sufficient exclosures to sample adequately the upper crowns of dense stands”. Effects of avian predation on insects in tree crowns and on canopy trees have never been explored.

II-1

Effects of avian predation on leaf-rolling lepidopterous larvae

Introduction

Predation is an important determinant of the abundance and distribution of prey organisms (Sih et al. 1985). Prey organisms avoid predations in various ways, e.g., morphological mimicry, behavioral escape, phenological escape (Pianka 1978, Sillén-Tullberg et al. 1982, Kinsman and Platt 1984). In particular, numerous insects developed nests or arranged host leaves as galls or rolls to avoid predations (Weis and Abrahamson 1986, Price and Clancy 1986). Many lepidopterous larvae, for instance, roll host leaves for defense against predators (Powell 1980). Although Damman (1987) showed that leaf rolls could decrease the risk of predation by carnivorous insects, we know little about the function of leaf rolls as a means of avoiding bird predations.

In forest ecosystems, insectivorous birds are known to be a major predator of lepidopterous larvae (Holmes et al. 1979, Price and Clancy 1986, Marquis and Whelan 1994). Birds are considered to visually scan the environment to forage on prey (Bell 1991). Heinrich and Collins (1983) showed that birds detect the larvae using the leaf damages. If the shape of the plant leaf arrangement made by lepidopterous larvae serves as a search image for the birds' hunt, the leaf roll can increase the risk of predation on the leaf rollers. Because many bird species can fold and forage on the leaf rolls (Remsen and Robinson 1990), it should be assessed whether the leaf-rolling behavior of lepidopterous larvae increases or decreases the risk of avian predators.

In this study, the interaction between lepidopterous leaf rollers and insectivorous birds on the lilacs was examined by two types of manipulative field experiments. Because birds are known to hierarchically search the environment to localize and locate prey, the bird foraging process can be divided into two phases: (1) the search for a feeding-patch, i.e., an individual lilac, and (2) the search for prey within a feeding-patch (Heinrich and Collins 1983). First, to determine the effect of leaf rolls on birds' feeding-patch localization, the responses of the bird to the removal of leaf rolls from the lilacs were measured. Then, to examine the prey selection within a feeding-patch, the mortalities of each leaf roller species induced by bird predation were measured in relation to their roll shapes.

Materials and Methods

Study area and animals

Field studies were performed in the TOEF during May to June, 1996. The canopy was dominated by maple (*Acer mono*), linden (*Tilia japonica*), and oak (*Quercus crispula*), with an admixture of spruce (*Picea jezoensis*), and with japanese lilac (*Syringa reticulata*) dominating the shrub layer (1 - 3 m in height).

On the lilac, there were three dominant lepidopterous leaf rollers: *Zelleria* sp., pylaridae sp. 1, and pylaridae sp. 2. (Murakami, personal observation). The larvae roll leaves of lilac in various shapes, which probably affect their conspicuousness to predators: *Zelleria* sp. completely rolled a pair of leaves together in the shape of a corn cob, pylaridae sp. 1 partially rolled a leaf, and pylaridae sp. 2 stacks one leaf upon another leaf (Fig. 1). There was no significant difference in the dry mass (dried at 60°C for 24 h and weighed to the nearest 0.01 mg) of individuals, which were collected from five randomly selected individuals of the lilacs on May 21, among

Zelleria sp. (1.26 ± 0.15 SE mg), pylaridae sp. 1 (1.94 ± 0.12), pylaridae sp. 2 (2.05 ± 0.089 ; $n = 30$ for all the three species, one-way ANOVA, $F = 1.382$, $df = 2,87$, $P = 0.27$).

In the forest, the lilacs buds broke on 3 May, when the leaf rollers emerged. The leaf rollers developed into identifiable species by one week after their emergence.

Experiment 1: the effect of leaf roll removal on bird searching for prey

To examine the effects of the presence of leaf rolls on prey searching by birds, all leaf rolls were removed from 10 lilac trees (1 - 2 m in height) on May 20, and another 10 intact trees were selected as the controls. Before the treatment, a two-way ANOVA did not detect a significant difference in the number of leaf rollers on the lilacs among *Zelleria* sp., (9.5 ± 1.13 SE), pylaridae sp. 1, (8.50 ± 1.29), and pylaridae sp. 2 (6.9 ± 1.19 ; $F = 2.44$, $df = 1,54$, $P = 0.124$), and between control (9.07 ± 1.19) and treatment (7.5 ± 1.21 ;) trees.

The visits by the four dominant birds was recorded on each of these trees every other day from May 21 to June 10. In each daily observation, I simultaneously observed five lilac trees nearby each for 0.5 h. This was repeated three more times at three other locations, so that all the 20 lilacs were observed in one day. I observed each individual tree for 5.5 h over the observation period. Data on the visiting frequency of the birds was expressed as the number of visits per hour for each lilac tree (referred to as the visitation rate).

Experiment 2: the effect of bird predation on leaf rollers

On 17 and 18 May, 10 randomly selected lilac trees were enclosed by cages of 15-mm mesh net that allowed all insects but no birds to pass. Another 10 unenclosed trees

were selected as the controls. Light attenuation by the net averaged 4%. The numbers of leaf rollers per shoot on each tree were surveyed separately for each roller species both at the beginning (18 May) and the end (10 and 11 June) of the experiment.

Statistical treatment

The differences in the visitation rate between treatment trees (leaf rolls absent) and control trees (leaf rolls present) were tested by one-way ANOVA for each bird species.

A two-way ANOVA was used to detect the effects of the bird removal on the number of leaf rollers with the treatment and the date as factors. Exact values were $\log_{10}$ transformed to standardize variances and improve normality, if necessary to satisfy the assumptions of ANOVAs (Sokal and Rohlf 1995). All statistical tests were two-tailed. For all tests, an alpha value of 0.05 was used for statistical significance.

Results

Experiment 1

The visitation rates in treatment trees were lower than those in control trees for both the great tit ($F = 4.953$, $df = 1,18$, $P = 0.039$) and the marsh tit ($F = 4.487$, $df = 1,18$, $P = 0.048$; Fig. 2). By contrast, no differences were evident in the visitation rate between the treatment and control trees for any of the flycatchers ($F = 3.301$, $df = 1,18$, $P = 0.086$) or warblers ($F = 2.250$, $df = 1,18$, $P = 0.15$). The great tit and marsh tit (tit species) were observed to forage on leaf rollers by unfastening the rolls, whereas the flycatchers and the warblers rarely foraged on the lilacs.

Experiment 2

A two-way ANOVA revealed significant effects of both treatment ($F = 14.99$, $df = 1,36$, $P < 0.001$) and time ($F = 35.16$, $df = 1,36$, $P < 0.001$) and on the number of *Zelleria* sp. (Fig. 3), with an interactions being also significant ($F = 9.442$, $df = 1,36$, $P = 0.004$). Significant time effect was encountered on the number of pylaridae sp. 1 ($F = 0.071$, $df = 1,36$, $P = 0.79$) and pylaridae sp. 2, ($F = 3.33$, $df = 1,36$, $P = 0.07$). The treatment and interaction effects were not significant in either species (pylaridae sp. 1; treatment, $F = 5.08$, $df = 1,36$, $P = 0.031$; interaction, $F = 0.15$, $df = 1,36$, $P = 0.90$; pylaridae sp. 2; treatment, $F = 5.59$, $df = 1,36$, $P = 0.02$; interaction, $F = 0.045$, $df = 1,36$, $P = 0.83$). These results indicate that avian predation influenced on the mortality of *Zelleria* sp. only, although the number of leaf rolls decreased in all the three species during the experimental period irrespective of the accessibility of birds.

Discussion

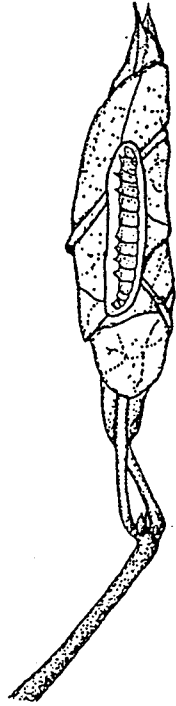
In the present study, two tit species, the great tit and the marsh tit, were observed to frequently visit the lilacs and unfasten the rolls and pick up the larvae. However, neither narcissus flycatchers nor crowned willow warblers visited the lilacs. Moreover, when the leaf rolls were removed from the lilacs, the visitation rate of these tit species declined (Experiment 1). These results revealed that the tits primarily visited the lilacs to forage on the leaf rollers. The presence of leaf rolls on the lilac tree probably serves as a cue for tit species to search a feeding-patch.

In experiment 2, the number of *Zelleria* sp. larvae decreased only under the presence of bird predation, whereas the mortality of the other two lepidoptera were not influenced by birds. Thus, the tits appeared to forage on *Zelleria* sp. larvae only. A number of factors, e.g., prey size, handling time, or the transparency of the

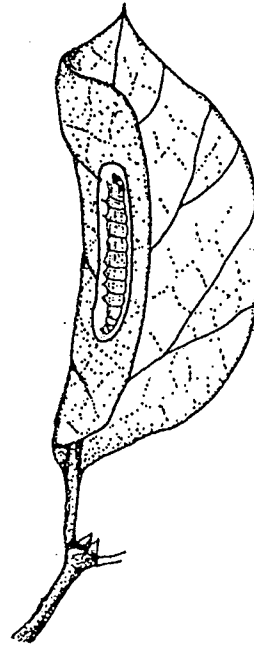
prey, should alter the prey selection by birds (Krebs et. al 1977, Heinrich and Collins 1983). In this study, however, there were no differences in body weight among the three leaf rollers. The birds' great preference for *Zelleria* sp. can not be explained by the larger prey size. Although I have no data on differences in the handling costs associated with unfastening different roll shapes, it is clear that the greatest effort is needed to unfasten the tightest roll of *Zelleria* sp. On the other hand, the shapes of leaf rolls, in terms of the extent of leaf modification, apparently differed among the leaf rollers (Fig. 1): *Zelleria* sp. altered the leaf form most greatly. The more the lilac leaves are altered, the easier it will be for birds to detect the leaf rolls. Thus, the great alteration of leaf arrangement by *Zelleria* sp. larvae could cause a higher risk of predation by birds. Birds (tit species in this study) utilized the presence of leaf rolls on the lilacs to localize a feeding-patch, i.e., an individual lilac tree, and used the altered leaves to locate the prey within the lilacs.

If a great alteration of leaf arrangement decreases the survival of leaf rollers, then the tight leaf rolling should provide another benefit to the larvae. Although the effects of parasitic arthropods, e.g., wasps and flies, which are the enemies on leaf rollers (Strong et al. 1984), were out of my scope, the tightly rolled leaves of *Zelleria* sp. may function as a better protection against arthropod enemies than the leaf roll arrangements of other rollers. Weis et al. (1992) examined the factors determining the size of leaf galls, which is another alteration of leaf tissues by herbivorous insects, and suggested that the optimal size of leaf galls of *Eurosta solidaginius* (Diptera) was determined as a compromise between adaptations against birds and parasitoid wasps. Birds preferred much more larger galls than parasitoid wasps. Moreover, Sagers (1992) suggested that the light intensity decreased by leaf-rolling enhances the quality of the leaves as a food resource of the larvae; fibre and tannin contents declined in shaded leaves compared with intact ones (Mole et al. 1988). The leaf rolls of *Zelleria* sp., which are the tightest of those examined, probably block light

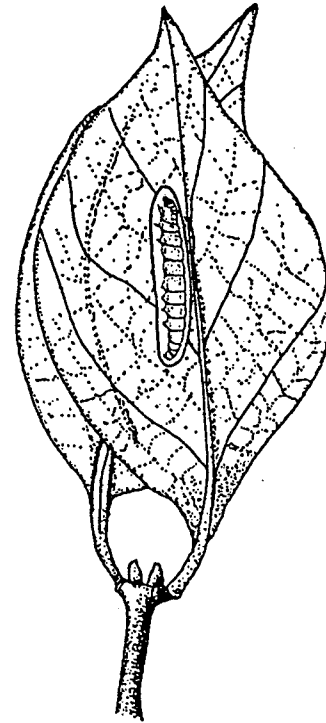
most effectively. Because many herbivorous arthropods face predation from multiple enemies as well as resistance from plants, a trade-off among these factors is important for a better understanding of the evolution of various leaf roll shapes.



Zelleria
sp.



pylaridae
sp.1



pylaridae
sp.2

FIG. 2-1-1. Leaf rolls of three lepidopterous species, with indication of the larval position.

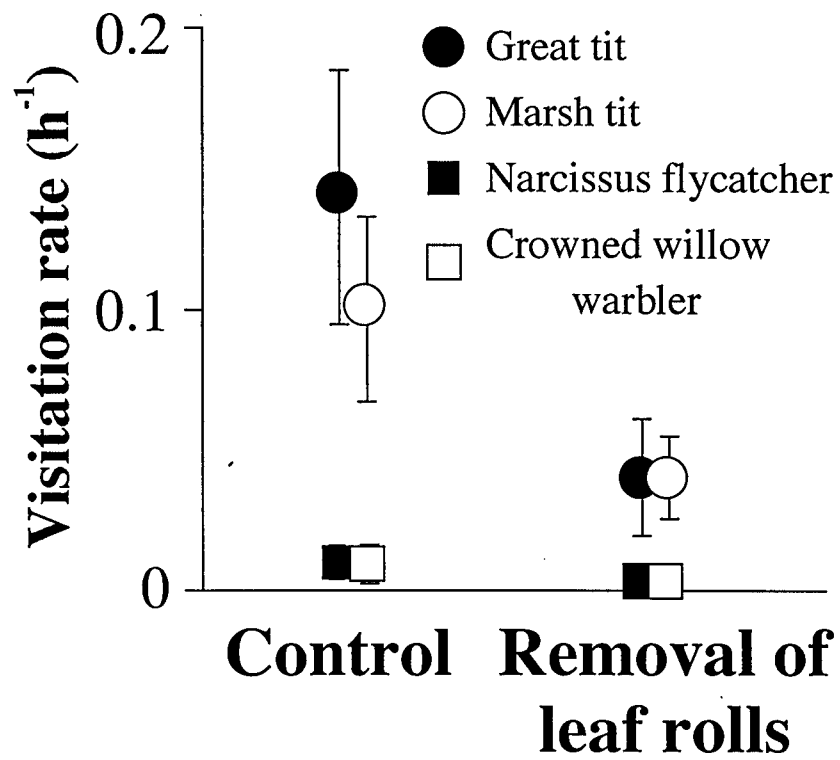


FIG. 2-1-2 Effects of leaf roll removal on the number of foraging visitation on a lilac tree per hour. Error bars are standard errors.

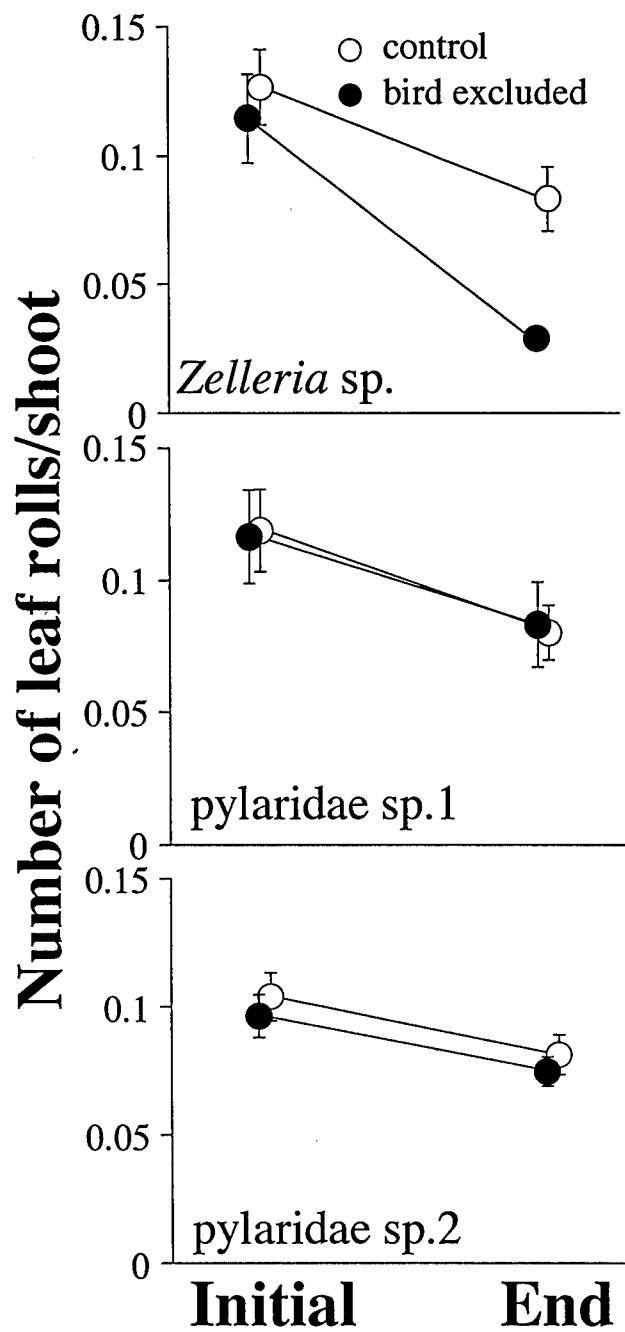


FIG. 2-1-3. Comparisons of numbers of leaf rolls between control and bird-excluded japanese lilac trees and between before and after the experiment, separately made for each of the three predominant lepidopterous leaf roller species. Error bars are standard errors.

II-2

Canopy enclosure experiment

Introduction

Predation effects extend through the trophic hierarchy (Mills et al. 1987). Certain models predict that the effect of top predators on producers depends on the number of trophic levels in the system: in a three-trophic-level system the effect is positive, whereas in a four-trophic-level system the effect is negative (Oksanen et al. 1981). These models assume that each consumer level eats only the next trophic-level down. In terrestrial systems with both top and intermediate predators, the top predators often feed on both intermediate predators and herbivores, particularly when the top predators are vertebrates and the intermediate predators and herbivores are arthropods (Schoener 1989). These complex trophic interactions, which may necessitate different models, may be common in forest ecosystems structurally complex with high canopies and more complex food webs (Spiller and Schoener 1996).

Birds are important insectivores in forest ecosystems and structure the lower trophic level communities (Holmes et al. 1979, Atlegrim 1989, Crawford and Jennings 1989, Gunnarsson 1994, Marquis and Whelan 1994). Several studies experimentally documented that birds reduced the number of prey insects feeding on plants (Holmes et al. 1979, Holmes 1990) and the leaf damages (Atlegrim 1989), and increased the plant growth (Marquis and Whelan 1994). However, forest passerine birds are quite divergent in their foraging methods and/or microhabitats (Norberg 1979, Wiens 1989). The roles of birds in forest ecosystems can vary from species to species.

I conducted a large-scale field experiment, manipulating the presence and the absence of two bird species within canopy enclosures, to determine the effects of birds on lower trophic levels, carnivorous arthropods, herbivorous arthropods, and plants. I hypothesized that foliage gleaning bird, great tit (*Parus major*), affects negatively herbivorous arthropods and positively plants (Fig. 2-2-1, Model A). On the other hand, bark gleaning bird, nuthatches (*Settica europaea*), was expected to have a negative effect on carnivorous arthropods, in particular ants, in turn a positive effect on herbivorous arthropods, and then a negative effect on plants (Fig. 2-2-1, Model B).

Methods

Experiment 1

In spring 1996, I made three canopy enclosures (15 x 15 m wide and 10 m high) with nylon cloth (17 mm mesh) in TOEF (Fig. 2-2-2). The study site was a secondary forest dominated by oak (*Quercus crispula*) with admixture of linden (*Tilia japonica*) and maple (*Acer mono*). The three enclosures contained 19, 18, and 16 oak trees, and 43, 42, and 39 trees of the other species more than 10 cm in diameter at breadth height and ca. 9 m in height.

Prior to the experiment, on June 6 to 8, I measured the initial conditions of the abundance of arthropods on foliage, that on tree trunks, and the leaf damage within the enclosures. Samples were taken from 15 oak trees for each enclosure. A foliage was cut at 50 cm from the end of branch for each oak tree and immediately put into a plastic sack. All the arthropods within the sack were collected later in the laboratory. Arthropods on tree trunk were sucked by a vacuum cleaner from ca. 1 m² surface of

bark for 3 minutes for each oak tree. The sampled arthropods were classified into three categories, lepidopterous larvae, ants, and others, and counted for each category. To assess the degree of leaf damage, 50 leaves were sampled from each tree. The sampled leaves were photocopied, and the original intact shapes were restored, but subjectively, with pencil. These actual and restored shapes of leaves were taken into a computer (Macintosh, Apple Co. Ltd.) by an image scanner (Hewlett-Packard) and the percentages of missing areas were measured to the nearest 0.1 % by NIH Image software.

On June 9, males of great tit and nuthatch were captured in the surrounding forest and immediately released into the enclosures. The first enclosure was installed with one bird of great tit (Great tit treatment), the second with one bird of nuthatch (Nuthatch treatment), and the third with no bird (Birdless treatment). The experimental bird density (one bird per $15 \times 15 \times 10 \text{ m}^3$) was approximately twice of the natural density of insectivorous passerine birds in the forest of the study site (Ishigaki and Matsuoka 1971). The experimental period was set to be ca. 2.5 weeks, since it is known that the number of lepidopterous larvae varies considerably in spring during about one and half month after the budbreak (Chapter I). On June 26 to 28, the same samplings as those before the experiment were made on the 15 selected oak trees in each enclosure.

I observed the foraging behavior of each individual of great tit and nuthatch within enclosures, and birds in the forest of 9 ha around enclosures for 2 hours every day respectively during the experimental period. The foraging site of each foraging maneuver was recorded and classified into three categories, Leaf, Twig and Trunk, and the other. The frequencies of each foraging site were not significantly different between inside and outside of enclosures for both bird species (χ^2 -test; great tit: $P = 0.066$; nuthatch: $P = 0.646$; Fig. 2-2-3). The great tit frequently foraged on leaf (ca.

75 % of total foraging maneuvers), whereas the nuthatch rarely foraged on leaf (ca. 25 %) and foraged on bark or twigs (ca. 75 %).

Experiment 2

In order to assess effects of ants on organisms at lower trophic levels independently from those of birds, an ant-excluding experiment was conducted in the forest nearby the enclosures. On June 11, ants were excluded from 15 oak trees within a 15 x 15 m quadrat by tanglefoot ring on the tree trunks at the height of ca. 1 m. The control quadrat was set in the neighborhood. The abundance of arthropods on foliage and the degree of leaf damage were measured for each quadrat on June 10 and 30.

Statistical analysis

A two-way ANOVA (factor = treatment, time) was used to detect effects of the experimental treatments on the number of arthropods in each category and the percentage of leaf damage. Effect of ants were also tested by a two-way ANOVA (factor = treatment, time). The numbers of lepidopterous larvae and ants were log transformed for the high skewness in the data, and the percentage of leaf damage was arc-sin transformed (Sokal and Rohlf 1995). All statistical tests were two-tailed.

Results

Experiment 1

Effects of the enclosure treatments on the numbers of arthropods were tested only for the lepidopterous larvae on the foliage and ants on the bark. Other categories of arthropods were very scarce on the foliage and/or on the bark. The effect of time on

the number of lepidopterous larvae on the foliage was significant, but that of treatment was not significant (two-way ANOVA; treatment: $F = 2.008$, $df = 2$, 84 , $P = 0.14$; time: $F = 117.5$, $df = 1$, 84 , $P < 0.001$; Fig. 2-2-4a). However, the significant interactive effect of treatment and time was detected on the number of lepidopterous larvae on the foliage ($F = 4.28$, $df = 2$, 84 , $P = 0.017$), meaning that the number of lepidopterous larvae was significantly reduced by great tit compared with the other treatments. Neither the effect of time nor that of treatment on the number of ants on the bark was significant (treatment: $F = 1.824$, $df = 2$, 84 , $P = 0.17$; time: $F = 0.35$, $df = 1$, 84 , $P = 0.56$; Fig. 2-2-4b). In this case, too, the interactive effect was significant: i.e., the number of ants was significantly reduced in the enclosure with a nuthatch ($F = 3.47$, $df = 2$, 84 , $P = 0.040$). On the leaf damage, the effects of time and treatment were both significant (treatment: $F = 82.16$, $df = 2$, 294 , $P < 0.001$; time: $F = 362.8$, $df = 1$, 294 , $P < 0.001$; Fig. 2-2-4c). The significant interactive effect of time and treatment ($F = 36.69$, $df = 2$, 294 , $P < 0.001$) indicates that the leaf damage was larger in the Birdless and Nuthatch treatments than in the Great tit treatment.

Experiment 2

On the bark, three ant species; *Mirmica* sp., *Lacius* sp., and *Formica japonica*, were dominant. In the ant-excluding experiment, effects of treatment and time were both significant on the number of lepidopterous larvae in the foliage (two-way ANOVA: treatment: $F = 7.02$, $df = 1$, 56 , $P = 0.011$; time: $F = 99.39$, $df = 1$, 56 , $P < 0.001$; Fig. 2-2-5a), with the significant interactive effect ($F = 4.83$, $df = 1$, 56 , $P = 0.032$). This means that the ant-exclusion resulted in the increase of the number of lepidopterous larvae in the foliage. On the rate of leaf damage, the treatment effect was not significant, but the time effect was significant (treatment: $F = 0.125$, $df = 1$, 56 , $P = 0.73$; time: $F = 45.3$, $df = 1$, 56 , $P < 0.001$; Fig. 2-2-5b), with the interactive effect

being not significant ($F = 2.56$, $df = 1, 56$, $P = 0.115$). The ant-exclusion did not affect the leaf damage.

Discussion

The enclosure experiment revealed that the presence of great tit reduced the abundance of lepidopterous larvae but did not affect the abundance of ants on the bark, whereas the presence of nuthatch *vice versa*. The abundance of lepidopterous larvae was 2.5 times higher in the Nuthatch and Birdless treatments than in the Great tit treatment. Such difference in the abundance of lepidopterous larvae was clearly reflected in the degree of leaf damage being 3 times higher in the Nuthatch and Birdless treatments than in the Great tit treatment. However, there were no differences in the number of lepidopterous larvae and the leaf damage between the Nuthatch and Birdless treatments. The behavioral observation within the enclosures revealed that great tit mostly foraged from leaf surfaces in the foliage (ca. 90% of the total foraging maneuvers), whereas nuthatch mainly foraged on tree trunks (ca. 70%) but occasionally in the foliage. Accordingly, great tit mostly fed on lepidopterous larvae on the foliage, whereas nuthatch consumed both ant on trunks and lepidopterous larvae on the foliage.

The negative effect of ants on lepidopterous larvae and in turn the positive effect on plants were confirmed by many studies conducted in temperate forests (Skinner 1980; Skinner and Whittaker 1981; Haemig 1992). For instance, Skinner and Whittaker (1981) showed that the presence of ant (*Formica rufa*) reduced the abundance of winter moth (*Operophtera brumata*) on limestone woods, and hence reduced the leaf damages. The ant-exclusion experiment, in this study, also revealed

that the existence of ants decreased the abundance of lepidopterous larvae, but did not affect the leaf damage. Because nests of ants were distributed quite heterogeneously on the forest floor, ants were not observed crawling up to all the experimental oak trees. This probably made the effect of ant-exclusion on the leaf damage unclear.

Pacala and Roughgarden (1984) indicated that if the presence of top-predator affects both intermediate predators and herbivores, their effects on plants become weak. In the present study, nuthatch probably affected lepidopterous larvae both directly by foraging on them and indirectly via ant consumption, and the net effect on plants became neutral.

These results confirm the predicted Model A for great tit and partly modified Model C for nuthatch (Fig. 2-2-1). Spiller and Schoener (1990b) revealed that the *Anolis* lizards reduced the leaf damage through consumption of herbivorous insects on button wood in Bahamian island. Atlegrim (1989) showed that insectivorous birds also had a positive effect on understory plants in Swedish forest. On the contrary, Carpenter and Kitchell (1988) showed that piscivorous fishes increased the biomass of zooplankton through consumption of planktonivorous fishes, and as a result reduced the biomass of phytoplankton. Spiller and Schoener (1990a) explained the different effects of top predators in food webs owing to the differences in the size ratio among trophic levels; the size differences between top predators and herbivores are greater in the freshwater system than in the terrestrial system. On the other hand, Oksanen (1988) suggested that the chain length of food web depends on the primary production. Such cascade effects were detected also in my experiment. The differences in foraging habitat and method between great tit and nuthatch produce the different path ways within a food web.

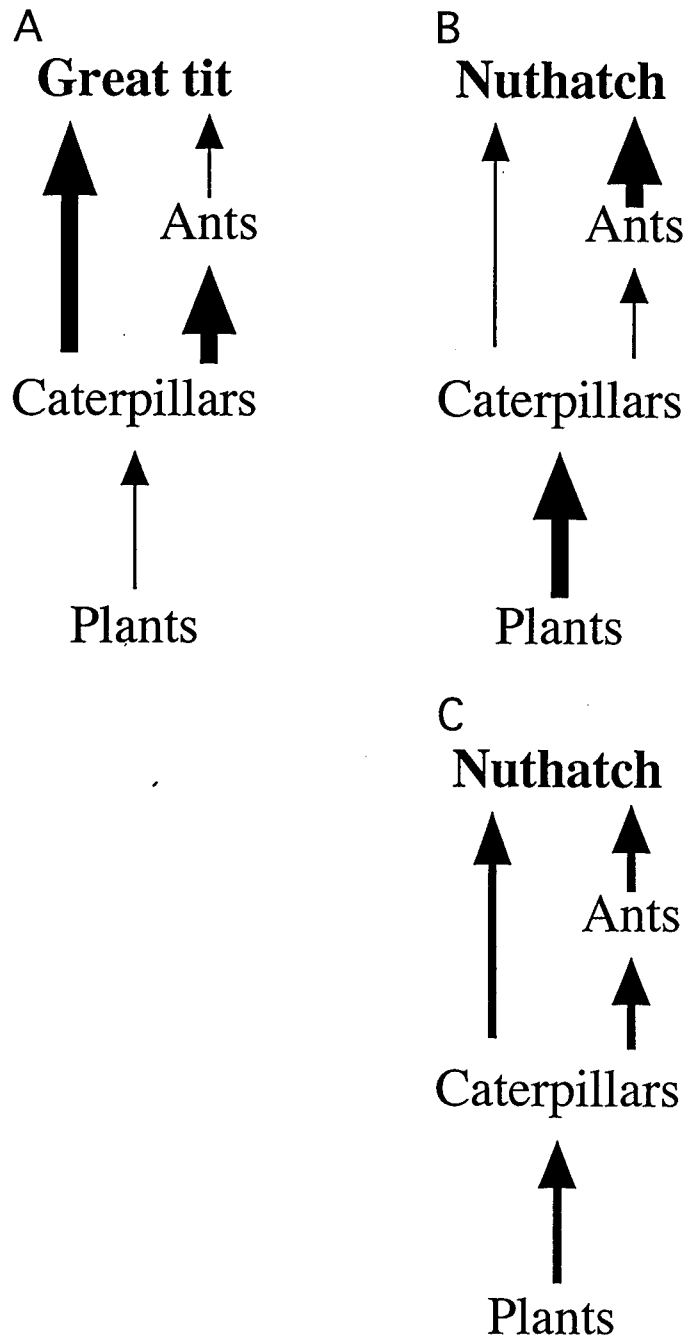


FIG. 2-2-1. Models for food chains leading to great titi (A) or nuthatch (B, C), as the top predator, with indication of the strength of their effects on each component; thick arrows indicating large effects, and thin arrows small ones.



FIG. 2-2-2. A photograph of canopy enclosure in June.

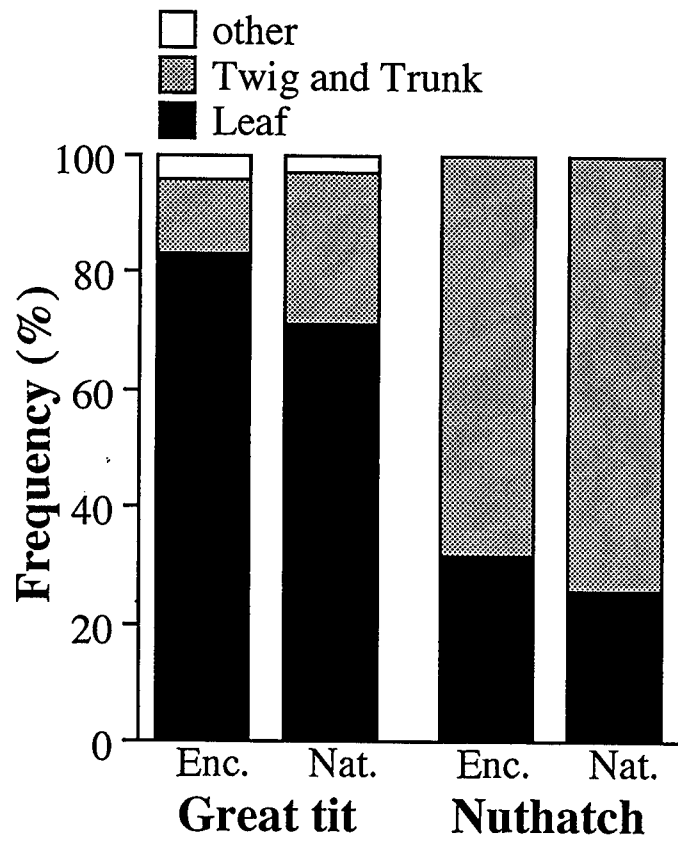


FIG. 2-2-3. Frequencies of each foraging site utilized by great tit and nuthatch within (Enc.) and outside (Nat.) of enclosures.

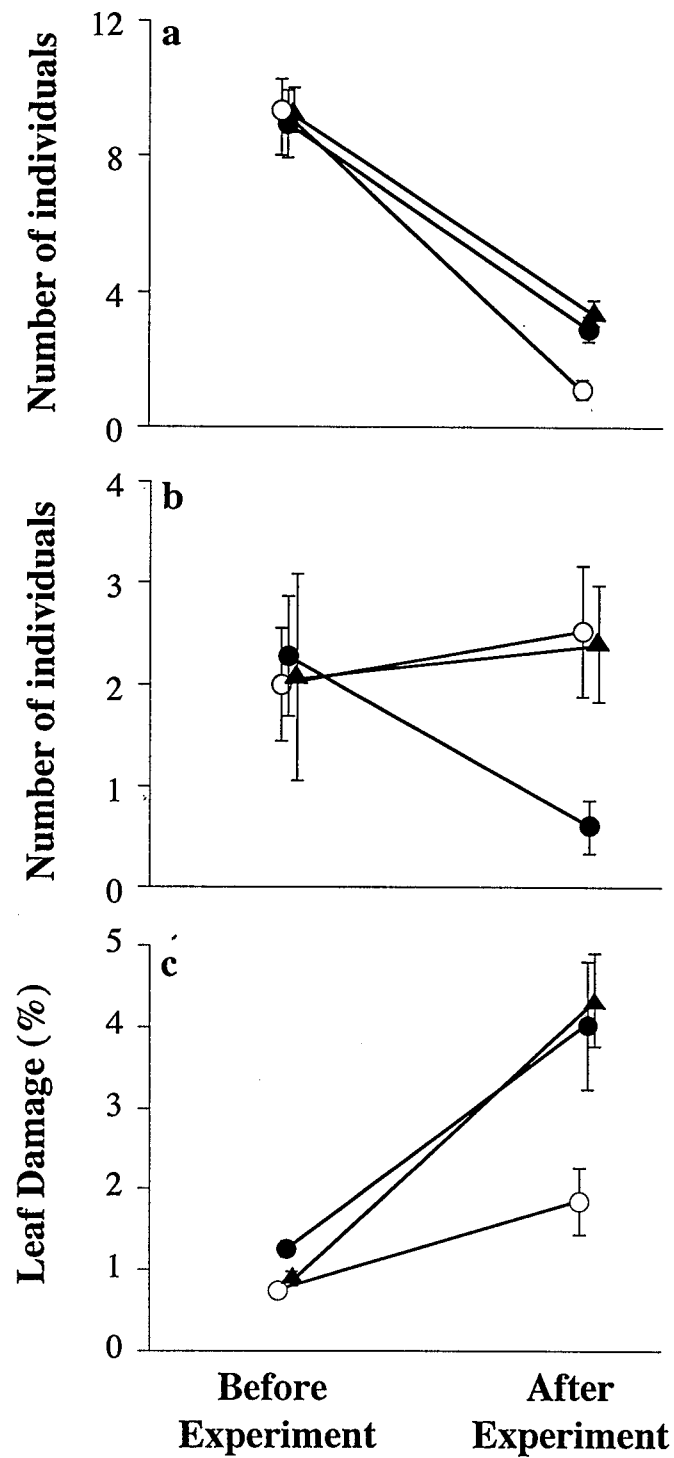


FIG. 2-2-4. Mean values of the number of lepidopterous larvae in the foliage (a), the number of ants on the bark (b), and the percentage of damaged leaf area (c), within the Great tit (O), Nuthatch (●), and Birdless (▲) enclosures. The values of before and after experiment were shown. Error bars are standard errors.

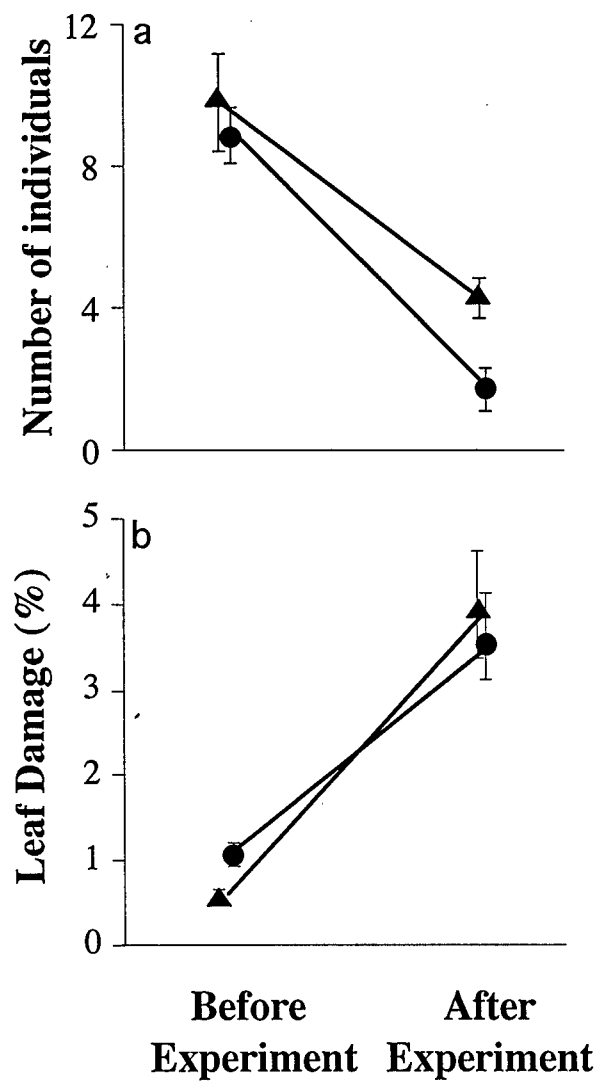


Fig. 2-2-5 Mean values of the number of lepidopterous larvae in the foliage (a) and the percentage of damaged leaf area (b), in the ant-exclusion (▲) and control stands (●). The values of before and after experiment are shown. Error bars are standard errors.

Conclusions

The present study revealed a complex network of biotic interactions among organisms in a temperate deciduous forest ecosystem. Many studies have demonstrated the close relationships between defense traits of plants and the survival and the growth of herbivorous insects (Feeny 1970; Rhoades and Cates 1976; Raupp and Denno 1983; etc.), and those between arthropod distributions and bird foraging behaviors (Greensberg 1987; Raley and Anderson 1990; Rosenberg 1993; etc.). However, connecting these two phenomena, the indirect effect of plant on bird have been less studied. Nordwijk et al. (1994) revealed a relationship between the timing of great tit breeding and the availability of spring-feeding lepidopterous larvae, which suggested that the timing of leaf emergence of deciduous trees indirectly affect the bird breeding phenology. In this study, I demonstrated the indirect effects of strengthening plant defenses on bird foraging behaviors via herbivorous insects (Fig. ii. A). The distribution and survival of lepidopterous larvae were strongly affected by the deteriorating quality of oak leaves in spring. Responding the changes in the abundance and distribution of lepidopterous larvae, birds shifted their foraging sites or prey types.

The effects in the inverse direction were also observed. First, the effect of avian predation on leaf-rolling lepidopterous larvae was shown (Fig. ii. B). The results of bird excluding experiment revealed that birds differently affected each leaf roller species. The differences in avian predation pressure on each leaf roller species only do not the role of the variation in shapes of leaf rolls. In this study, it is suggested that the shape of leaf roll is a compromise among adaptations to different stresses, e.g., plant resistance and attack of insect predator or parasite. In the other system, a species of geometrid moth, *Nemoria arizonaria*, feeds on different parts of

arizona oak (*Quercus arizonica*), catkins (staminate flowers) and leaves (Greene 1989). Larvae feeding on catkins develop into mimics of the catkins, whereas those on leaves mimic the first-year oak twigs. This polymorphism is caused by the difference in the amount of tannins in the diet: the high concentration of tannins in leaves induces the twig morphs. The high predation pressure by visually searching predators, such as birds, likely exerts strong selection for the high degree of cryptic morph. The present study shows the importance of synergetic effects of top-down and bottom-up forces in the mediation of behavioral or morphological features of organisms.

The studied bird species showed specific responses to the spatio-temporal fluctuation in the abundance and distribution of resources according to their foraging tactics, and inversely, had specific top-down effects on the lower trophic levels. In the last section, I showed the functional difference between bird species owing to their foraging habitat and method, which produced the different path ways within a food web (Fig. ii. C).

It is also suggested that herbivorous insects and birds influence the abundance or distribution of plants. Wada and Murakami (in submit.) showed that the recruitment of young oak trees was strongly affected by conspecific adult neighbors; saplings suffered from severe herbivory by lepidopterous larvae beneath adult trees. The resistance of canopy trees to herbivorous insects indirectly affected the survival of their offspring. Moreover, insectivorous birds can enhance the growth of oak saplings consuming herbivorous insects. The survivals and distributions of seeds, seedlings, and saplings should be studied in relation to defense system of canopy trees, herbivorous insects, and insectivorous birds to evaluate the Janzen-Connell hypothesis that density- or distance-dependent effects of natural enemies play a major role in spacing of forest trees (Janzen 1970; Connell 1971). This study suggests that narcissus flycatcher, in particular, plays an important role as guardians

shifting their foraging habitat from the canopy to the forest floor when herbivory against saplings is intensified by lepidopterous larvae spinning down from the canopy. Thus, forest insectivorous birds have direct and indirect effects in structuring of arthropod and plant communities, respectively.

Hunter and Price (1992) suggested that a synthesis of top-down and bottom-up forces in communities depends upon understanding of interactions between heterogeneous forces at all trophic levels. The present study focused on the variability and versatility in the system composed of insectivorous passerine birds, carnivorous and herbivorous insects, and plants. Temporal, spatial, and behavioral heterogeneity among and within ecosystem components has a considerable importance in structuring of natural communities. Further investigations are needed to understand such problems as how these complexities in interaction networks lead to the diversity or stability in forest ecosystems.

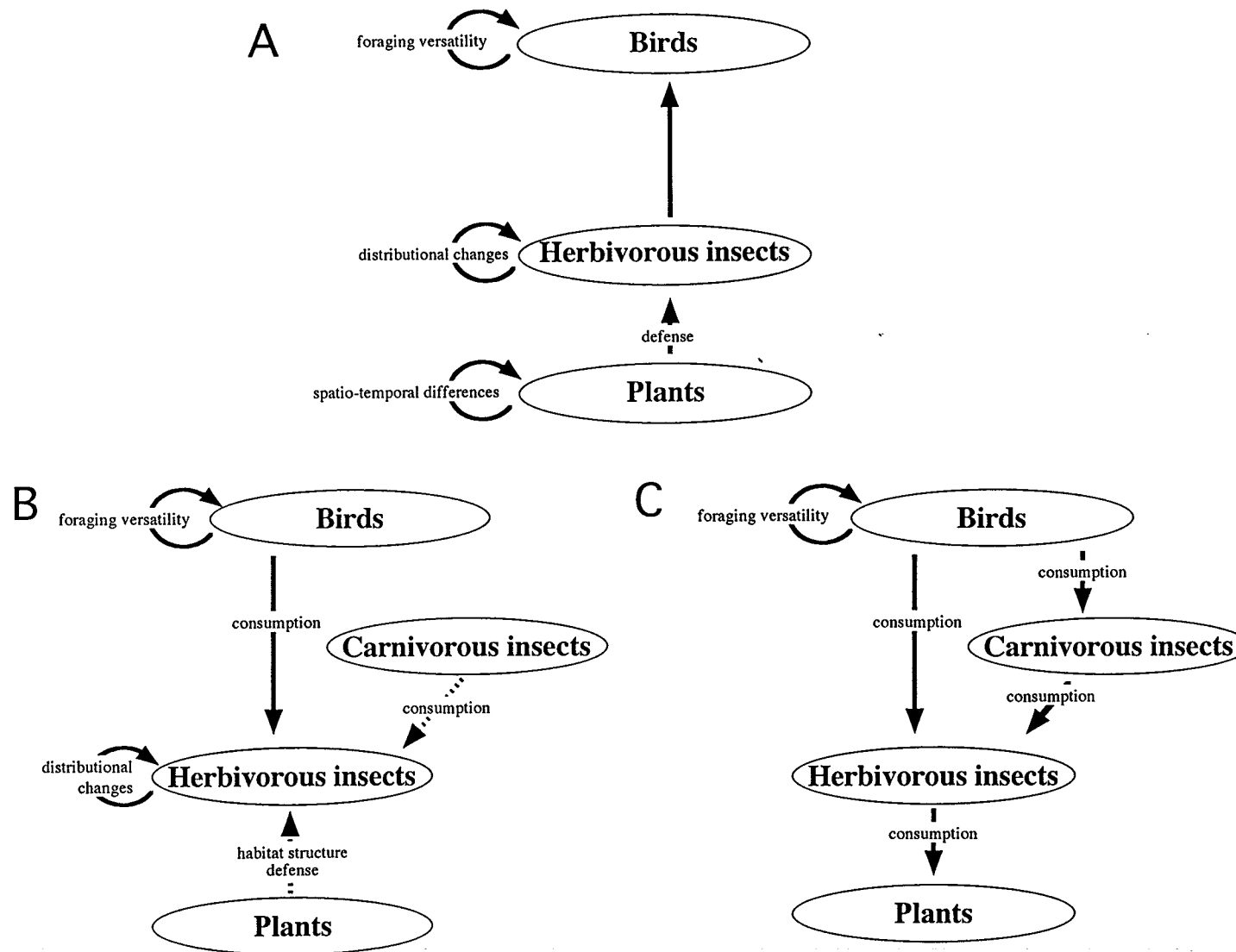


FIG. ii. Representations of observed interactions among plant, herbivorous insects, carnivorous insects, and birds in the present study. Effect of plant on bird via herbivorous insects (A), synergetic effects of bird, carnivorous insects, and plants on herbivorous insects (B), and effect of bird on organisms of lower trophic levels (C) were separately shown. Dashed lines indicate interactions which did not examined in this study.

Acknowledgments

I thank M. Toda for valuable comments and critical readings on drafts of this manuscript. T. Kohyama, S. Higashi, and T. Ohgushi gave me useful suggestions. S. Nakano reviewed this manuscript. Special thanks are due to K. Yoshida, Tomakomai City Museum, for useful information. T. Aoi, T. Hiura, and other staff members and students of Tomakomai Experimental Forest, Hokkaido University, supported field works. I also thank members of Biodiversity Group, Institute of Low Temperature Science, for their kindness during my works.

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Appendix

Numbers of lepidopterous larvae collected from the oak canopy, by sheet traps, and on the forest floor.

Family	Species	Oak Canopy	Sheet Traps	Forest Floor
Lycaenidae	<i>Chrysozephyrus brilliantinus</i>	3	-	-
Noctuidae	<i>Cosmia exigua</i>	17	43	32
	<i>Cosmia</i> sp.	-	2	2
	<i>Orthosia paromoea</i>	1	3	1
	<i>Perigrapha hoenei</i>	1	2	8
	<i>Telorta edentata</i>	18	49	35
	<i>Conistra ardescens</i>	5	2	-
	<i>Conistra grisescens</i>	3	1	-
	<i>Conistra unimacula</i>	5	35	34
	<i>Teratoglaea</i> spp.	11	10	45
Lymantriidae	<i>Lymantria dispar</i>	1	-	-
	<i>Lymantria monacha</i>	3	-	-
Geometridae	<i>Inurois fumosa</i>	34	87	16
	<i>Inurois</i> sp.1	32	5	3
	<i>Inurois</i> sp.2	3	-	-
	<i>Inurois</i> sp.3	7	-	-
	<i>Erannis golda</i>	5	-	-
	<i>Larerannis orthagrammaria</i>	2	7	15
	<i>Phigaliohyberria fuluinfula</i>	3	-	-
	<i>Colotois pennaria</i>	4	-	-
	<i>Cystidiatrun cangulata</i>	-	4	-
	<i>Eupithecia</i> sp.1	5	1	5
	<i>Eupithecia</i> sp.2	7	4	-
	<i>Eupithecia</i> sp.1	3	-	-
	<i>Idiotephria evanescens</i>	7	18	-
	<i>Euchoecan ebulata</i>	-	1	-
	<i>Operophtera brumata</i>	16	1	2
	<i>Asthena nymphaeata</i>	25	-	-
	<i>Asthena</i> spp.	27	9	6