

カラムツハラアカハバチ(Prisifora erichsoni)幼虫に対する鳥類の捕食活動の増大

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短 報

Increase in Foraging Activity of Birds as Predators on the Larvae of the Larch Sawfly, *Pristifora erichsoni* (Hymenoptera, Tenthredinidae)*

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I. Introduction

The role of birds as predators of forest insects generally is considered negligible in the epidemic stage of outbreaks (3, 11, 12). But both numerical and functional responses of birds occur, and in some cases, birds play a significant role in controlling insect populations (7, 9). Regarding the larch sawfly, BUCKNER and TURNOK (1) showed that bird predation is a significant factor in the regulation of the sawfly population to low densities and perhaps up to moderate infestation levels. Thus it is important to indicate whether numerical and/or functional responses occur under various conditions concerning the expansion of the area infested by a pest, its location, outbreaking level, avifauna, and so forth. Further more, as most of studies on bird predation were conducted in vast, uniform, coniferous plantations in North America and Europe, it is interesting to describe a situation in a mosaic distribution of stands accompanied by complicated topography in Japan. This study reveals an easy method to estimate both numerical and functional responses of birds, and shows what species and how they actually responded to outbreaks of the sawfly.

The Kiso District is located in the southernmost part of the larch sawfly's distribution range (15). In this area, it started proliferating in young larch (*Larix kaempferi*) stands at about 1,400 m above sea level in 1975, and lasted for four or five years in the same larch stands. It rapidly increases in numbers and then gradually decreases within a year or two. The infested area shifted north and northwest, descending in altitude, and reached the Kuinohara District in 1983 (14). Each year, a new outbreak was found in a few stands, and the total infested area was less than twenty ha.

II. Outbreak of the Larch Sawfly in 1983 and 1984

At Kuinohara, the first instar larvae of the larch

sawfly were observed first about August 10 in 1983 in larch stands (HAMA and OZAWA, pers. com.), and continued until early September. Thus they were available to birds for only a short time. This situation contrasted with that at Manitoba, Canada, where occurrence was for more than three months (1), and at Hokkaido (5). The duration of outbreaking in 1984 was almost the same as that in 1983. In 1984, the volume of fallen frass created by the larvae was measured as dry weight every three days, and the peak period of their defoliation activity was estimated to be from the 23rd to the 26th of August (unpublished data). The total volume of foliage eaten was estimated to be 486 kg/ha; this is about a third or a fourth of the entire foliage in a closed larch stand (using the digestion rate of 1.38 reported by HIGASHIURA (4)). In 1983, almost all of the foliage was consumed by larvae on August 26. Thus it was concluded that the density of the sawfly in 1984 was about a third or a fourth of that in 1983.

III. Study Areas

Census lines and census quadrats were established at three sites. Kuinohara was the site of the larch sawfly outbreak, and the others, Nanguh-jinja and Oh-hara, were the control ones where the sawfly outbreaking had already disappeared (14).

At Kuinohara (35°52'N, 137°43'E, 900 m altitude), the census line was 325 m in length. Two circle quadrats were established in mature larch plantations and were 0.0908 ha ($r=17$ m) and 0.0531 ha ($r=13$ m) in area. They were located on slopes facing southwest. The vegetation along the census line were mixed plantations of conifers with little understory (about 35% of area), broadleaved deciduous forests with moderately dense understories (30%), and larch plantations. The first was composed of *Chamaecyparis obtusa*, *Cryptomeria japonica*, *Pinus densiflora*, *Abies firma* and *L. kaempferi* 20 to 25 m in height. The larch here also was defoliated by the sawfly larvae.

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The second was composed of *Quercus serrata*, *Prunus lannesiana*, *Acanthopanax sciadophylloides*, *Acer palmatum*, *Parabenzoïn praecox*, and others. The sawfly occurred here first in 1983.

At Nanguh-jinja (35°53' N, 137°47' E, 950 m altitude), the census line was 1,000 m in length, and the three quadrats in larch plantations were each 0.125 ha (25 m × 50 m). This site was located at the bottom of a shallow valley and along a stream. The vegetation along the line were plantations of *L. kaempferi* (about 60%), *C. japonica*, and *A. firma*, with some understory. Here, larch sawfly outbreaks occurred from 1977 to 1981.

At Oh-hara (35°50' N, 137°46' E, 1,100 m altitude), the census line was 275 m in length, and the three quadrats in larch plantations were each 0.125 ha (25 m × 50 m). The vegetation along the line were *L. kaempferi* with some understory (about 60%) and *P. densiflora* with little understory. Some scattered summer cottages were located here. The sawfly outbreaks occurred from 1977 to 1980.

IV. Methods

Two kinds of censuses were conducted. A line census was used to estimate the relative density on each site, and this was regarded as the indicator of the numerical response. A quadrat census was used to estimate the height of the foraging activity as the functional response multiplied by the numerical one. The results were compared by a 2 × 2 matrix-like way; sawfly vs. non-sawfly places and sawfly-occurring vs. non-sawfly-occurring seasons (Tables 1 and 2). This enabled us to estimate the site effects and to omit them.

Censuses were conducted in late August of 1983 and 1984, when the sawfly larvae were present, and in late July in both years, except at Kuinohara in late September, 1983, when sawflies were absent. In a line census, the investigator, the same person for all censuses, walked by about 1 to 1.5 km/hr along the census line and recorded the species and number of birds observed within 25 m of the line on both sides (at Kuinohara and Oh-hara) or on one side (at Nanguh-jinja). To obtain an adequate sample line length of about 2 km in a period, observation walks were made twice in the same morning or more (up to seven times), within 2.5 hours after sunrise. A few censuses were conducted in a light rain, but their results were not different from the others, so that the effect of weather was not considered. Calculation of relative density (d_R ; number of birds per ha) was made by the following formula:

$$d_R = (N \times 10,000) / (L \times W)$$

where N is the number of individuals observed in

each census, L is the length of the census line, and W is the width of the belt transect in meter ($W=50$ at Kuinohara and Oh-hara, $W=25$ at Nanguh-jinja).

In a quadrat census, the investigator stayed ten minutes beside or in the quadrat and recorded bird species, number of birds, and the behavior of each individual. Observations were started after the line census, and continued, the investigator moving from one quadrat to another, until late afternoon. Calculation of foraging activity (d_F ; number of birds per ha per ten min) was as follows:

$$d_F = N / (T \times A)$$

where N is the number of individuals observed in foraging activities, T is the total time of ten-minute observations made in a day, and A is the quadrat area in hectares.

V. Results

1. Relative density

Results of line censuses indicated that the relative densities were not significantly different between places or seasons, during each year, except for the two differences between the densities at Nanguh-jinja and at Oh-hara in 1984 (Fig. 1 and Table 1). Both of these were data of places without the sawfly (O7, N8, and N7), and the differences were caused mainly by the low density at Oh-hara in July (O7). In 1984, density at any place was lower than that at the same place in 1983, and this was perhaps so because the 1983~1984 winter was extremely cold and long. Site characteristics of Oh-hara (higher altitude than the others) might

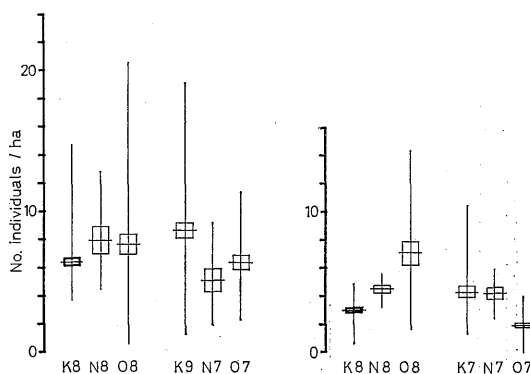


Fig. 1. Relative densities of birds in 1983 (left) and 1984 (right)

K8, Kuinohara in August when the sawfly occurred; N8, Nanguh-jinja in August; O8, Oh-hara in August; K9, Kuinohara in September; N7, Nanguh-jinja in July; O7, Oh-hara in July

Vertical bars, rectangles, and horizontal bars indicate ranges, standard errors, and means, respectively.

Table 1. Results of *t*-test in relative densities of birds in 1983 and 1984

Mean±S.D.	K 8	N 8	O 8	K 9	N 7	O 7
	6.39±3.17	7.90±3.76	7.62±5.82	8.62±6.65	5.10±3.21	6.38±3.88
1983	K 8	—	(12)	(16)	(12)	(16)
	N 8	NS	—	(10)	(6)	(10)
	O 8	NS	NS	(16)	(10)	(14)
	K 9	NS	NS	—	(12)	(16)
	N 7	NS	NS	NS	—	(10)
	O 7	NS	NS	NS	NS	—
Mean±S.D.	K 8	N 8	O 8	K 7	N 7	O 7
	3.00±1.56	4.50±1.10	7.07±5.19	4.31±3.46	4.20±1.68	1.93±1.54
1984	K 8	—	(10)	(5)	(14)	(18)
	N 8	NS	—	(5)	(10)	(14)
	O 8	NS	NS	—	(8)	(5)
	K 7	NS	NS	—	(10)	(8)
	N 7	NS	NS	NS	—	(14)
	O 7	NS	**	NS	NS	—

** $p < 0.01$; NS, not significant; numbers in brackets are degrees of freedom.

For the research numbers, see foot notes in Fig. 1. Note that K8 is the sawfly occurring stand.

Table 2. Results of *t*-test in foraging activities of birds in 1983 and 1984

Mean±S.D.	K 8	N 8	O 8	K 9	N 7	O 7
	76.80±19.03	0.17±0.29	13.52±2.16	14.80±17.74	0	0
1983	K 8	—	(3)	(3)	(6)	(3)
	N 8	**	—	(2)	(2)	(2)
	O 8	**	**	(3)	(2)	(2)
	K 9	**	NS	—	(3)	(3)
	N 7	**	NS	**	—	(3)
	O 7	**	NS	NS	/	—
Mean±S.D.	K 8	N 8	O 8	K 7	N 7	O 7
	6.86±9.12	0.76±1.32	3.24±2.01	0.81±1.02	0.70±0.84	0
1984	K 8	—	(3)	(3)	(3)	(3)
	N 8	NS	—	(3)	(2)	(2)
	O 8	NS	NS	(3)	(2)	(2)
	K 7	NS	NS	—	(6)	(3)
	N 7	NS	NS	NS	—	(5)
	O 7	NS	NS	NS	NS	—

** $p < 0.01$; NS, not significant; numbers in brackets are degrees of freedom.

For the research numbers, see foot notes in Fig. 1. Note that K8 is the sawfly occurring stand.

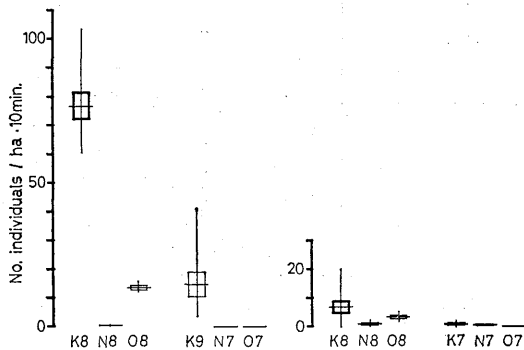


Fig. 2. Foraging activities of birds in 1983 (left) and 1984 (right)

See notes in Fig. 1.

Vertical bars, rectangles, and horizontal bars indicate ranges, standard deviations, and means, respectively.

be the cause of the very low density in July 1984. Considering its site conditions and that densities at Kuinohara were similar in sawfly-occurring and non-occurring seasons, the bird density in the infested district of Kuinohara was not higher than those at the other sites in both years.

2. Foraging activity increase

The results of quadrat censuses are shown in Figure 2 and Table 2. In 1983, the foraging activity of birds in the sawfly infested stand at Kuinohara in August (K 8) was much higher than those at the other sites or in other times. As the activity densities estimated at Nanguh-jinja in August and July, and at Oh-hara in July (N 8, N 7, and O 7) were almost negligible, they were significantly lower than that at Oh-hara in August (O 8). But this results might be due to the small sample size. The especially high foraging activity of K 8 could be regarded as the bird's response to

Table 3. Changes in foraging activities of birds between sawfly occurring season and non-occurring season at Kuinohara in 1983

Species	Activity in August* (Sawfly occurring)	Activity in September* (Sawfly non-occurring)
<i>Aegithalos caudatus</i>	2.72	0.16
<i>Parus major</i>	1.18	0.14
<i>P. montanus</i>	0.68	0.13
<i>P. ater</i>	0.53	0.19
<i>Phylloscopus borealis</i>	0.18	0.14
<i>Garrulus glandarius</i>	0.13	0.02
<i>Parus varius</i>	0.09	0.06
<i>Hypsipetes amaurotis</i>	0.08	0
<i>Dendrocopos kizuki</i>	0.06	0.03
<i>Muscicapa sibirica</i>	0.01	0.02
<i>M. griseisticta</i>	0	0.06

* No. of foraging individuals per ha per ten min.

the high density of prey, the larch sawfly larvae. The activity of K 8 was five times greater than that of K 9.

In 1984, none of the site-and-time combinations revealed significant difference in the foraging activity of birds. At the sawfly-occurring stand (K 8), the activity was slightly higher than those at the others, but it is not clear whether the birds responded to the moderate density of the sawfly in 1984.

3. Major predator species

Sixty-four species of birds were observed around the study area during the study period in the two summer seasons. Of these, nine species were recorded foraging in sawfly infested stands (Table 3) in 1983, and it was certain that they almost exclusively hunted larch sawfly larvae in the crowns of larch trees. For the long-tailed tit (*Aegithalos caudatus*) the foraging activity was 17.4 times as great in the infested stand as that in the same stands when the sawfly disappeared in September. For the great tit (*Parus major*) it was 8.4 times, for the willow tit (*P. montanus*), 5.4 times; for the coal tit (*P. ater*), 2.8 times, and for the jay (*Garrulus glandarius*), 8.0 times. In 1984, five species were observed hunting the sawfly, but a remarkable increase (six times) in foraging activity was recorded only for *P. major*. The responses of these five species to the high density of the sawfly were apparent. All of them were resident species, and the foraging groups seemed to be family flocks.

VI. Discussion

As MORRIS (11) wrote, "the most effective species of predators affecting an animal population are likely to be those that show a response to changes in its density," that is, a numerical response.

Then, it is one of the essential approaches to distinguishing functional responses of the predators from numerical ones.

The functional response is a change of the predation rate of each individual predator to the change of the prey density. HOLLING (6) counted the cocoons attacked by small mammals and estimated the number of prey per predator per unit time. His method is the best if the latter estimation is accurately possible; the predations are recognized easily and moreover, can be classified as to species of predator. But this is not possible in the situation of birds foraging for sawfly larvae on tree branches. Gizzard-content analysis (1, 9) is one method, and it has some drawbacks. Shooting predators may have a great impact on the predator populations; the samples are biased as to the shooting range and time, and it is very hard to obtain sufficiently large enough samples. An all-day quadrat census, by which we estimated the foraging activity in this study, is rather easy to conduct, and it was shown that a functional response with a numerical one can be estimated roughly with it, although the feeding efficiency of each individual bird is left to be estimated in the field or experimentally.

The practical methods in estimating bird numbers are the plot mapping of breeding pairs (1, 11) and the line census to estimate relative density (this study, 10). The major advantage of the latter is its simplicity. Changes in the estimated numbers were regarded as numerical responses, but this is not exactly right. In its primary meaning, the numerical response of predators should ideally be estimated by an increase in the number of identified individuals as a result of an increase in prey density. Without these data, we cannot completely exclude the existence of a numerical response in this study.

In the Kiso District, the lack of a numerical response of birds readily had been predicted because the area of the stands defoliated by the sawfly was small, and the period of larvae occurrence was as short as two weeks. This study suggests that some of the birds are able to respond quickly as they concentrate their foraging activity in newly infested stands. A significant increase in foraging activity was observed only in a stand of a remarkable sawfly outbreak with almost all of the larch defoliated. In a moderately infested stand, the increase in foraging activity was not significant, but greater activity was recognizable.

It is not possible to decide the effect of birds on the sawfly population until the mortality due to the birds is estimated. However, as there was no

remarkable numerical response, the effect of the bird predation was not very large. A five-fold increase of foraging activity may have some impact on the sawfly population, and there may be an indirect effect that makes the sawfly larvae fall before they grow into their fourth instars or increase their mortality while on the tree.

In addition to the on-branch foragers, the pheasant (*Phasianus colchicus*) possibly preys on the fallen larvae and cocoons on the ground (2 cited in 1). This species was one of the popular resident birds near the investigation sites in the Kiso District, although we could not directly observe its foraging activity.

The larch sawfly outbreak in Kiso was characterized by the smallness of the infested area, the shortness of the occurring period, and at a time of the highest bird density of the year after the bird breeding season. All of the major predator birds were residents. In such a situation, a remarkable numerical response cannot be expected, and it is desirable to maintain the bird populations as high as possible for the control of insect pests. Three of the five major predator species, *P. major*, *P. montanus*, and *P. ater*, are cavity nesters, well known to be restricted in number due to the shortage of nest sites, especially in artificial forests (13). Mortality of resident birds is high in winter due mainly to the shortage of food (8). Therefore providing nest boxes and winter feeding may be effective for forest pest control.

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