

# Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream

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## SUMMARY

1. The annual input, contribution to the diet of salmonids, and quantitative input of terrestrial invertebrates to four reaches with contrasting forest ( $n = 2$ ) and grassland riparian vegetation ( $n = 2$ ) were compared in a Japanese headwater stream.
2. The annual input of terrestrial invertebrates falling into the forest reaches (mean  $\pm 1$  SE =  $8.7 \times 10^3 \pm 0.3 \times 10^3$  mg m<sup>-2</sup> year<sup>-1</sup>) was 1.7 times greater than that in the grassland reaches ( $5.1 \times 10^3 \pm 0.8 \times 10^3$  mg m<sup>-2</sup> year<sup>-1</sup>), with clear seasonality in the daily input of invertebrates in both vegetation types. The daily input, however, differed between the vegetation types only in summer, when it rose to a maximum in both vegetation types.
3. Fish biomass also differed among the seasons in both vegetation types, being less in the grassland reaches. The contribution of terrestrial invertebrates to the salmonid diet in the forest and grassland reaches was 11 and 7% in spring, 68 and 77% in summer, 48 and 33% in autumn, and 1 and 1% in winter, respectively. The prey consumption rate of fish, which was similar between the vegetation types, increased with stream temperature and was highest in summer. Terrestrial invertebrates supported 49% (mean  $\pm 1$  SE =  $5.3 \times 10^3 \pm 0.4 \times 10^3$  mg m<sup>-2</sup> year<sup>-1</sup>) of the annual, total prey consumption ( $10.9 \times 10^3 \pm 1.7 \times 10^3$  mg m<sup>-2</sup> year<sup>-1</sup>) by salmonids in the forest and 53% ( $2.0 \times 10^3 \pm 0.3 \times 10^3$  mg m<sup>-2</sup> year<sup>-1</sup>) ( $3.8 \times 10^3 \pm 0.6 \times 10^3$  mg m<sup>-2</sup> year<sup>-1</sup>) in the grassland reaches.
4. Salmonids were estimated to consume 51 and 35% of the annual total (falling plus drift) input of terrestrial invertebrates in the forest and grassland reaches, respectively. The input of terrestrial invertebrates by drift, however, was almost equal to the output in both vegetation types, suggesting that the reach-based, in-stream retention of terrestrial invertebrates almost balanced these falling in.
5. Difference in the riparian vegetation, which caused spatial heterogeneity in the input of terrestrial invertebrates, could play an important role in determining the local distribution of salmonids.

**Keywords:** allochthonous input, food web subsidies, riparian vegetation, stream fish, stream–forest ecotone

## Introduction

Spatial movements of nutrients, detritus and prey organisms across the interface of contiguous habitats can influence the dynamics of consumer populations via 'bottom-up' forces in ecosystems (Polis *et al.*, 1996;

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Polis, Anderson & Holt, 1997). In particular, consumers in habitats where primary productivity is relatively low (recipient habitats) are often subsidized by the transport of food resources from more productive donor habitats, when sufficient trophic connectivity is maintained (Polis *et al.*, 1997). The spatial and temporal heterogeneity of such an allochthonous resource input may play a more important role in determining the distribution and dynamics of animal populations than autochthonous resources (e.g. Greenstone, 1983; Gray, 1993; Polis & Hurd, 1995; Rose & Polis, 1998).

The 'river continuum concept' proposes that riparian zones play a major role in the regulation of energy flow and nutrient cycling in forested headwater streams (Vannote *et al.*, 1980; Ward *et al.*, 1998). In headwater streams of temperate deciduous forests, for instance, the input of allochthonous plant detritus from riparian ecosystems has long been recognized as providing the most important trophic basis of stream food webs (Naiman & Décamps, 1997; Wallace *et al.*, 1997). This plant detritus is the principal food resource for secondary production of benthic invertebrates which, in turn, is used by organisms feeding at higher trophic levels, such as fish (Minshall, 1967; Kaushik & Hynes, 1971; Cummins, Cushing & Minshall, 1995; Wallace *et al.*, 1997). However, recent studies have provided insights into the significance of terrestrial invertebrates, which represents a relatively high-quality food resource (being directly consumed) for stream fishes (Mason & MacDonald, 1982; Garman, 1991; Cloe & Garman, 1996; Edwards & Huryn, 1996; Wipfli, 1997).

The contribution of terrestrial invertebrates to the diet of stream fish can be considerable, particularly in summer, which is characterized by a low biomass of benthic invertebrates (the alternative prey) but by a peak in terrestrial prey (Hynes, 1970; Garman, 1991; Nakano *et al.*, 1999b). Terrestrial invertebrates occasionally comprise 50–90% of fish diet during summer and are often preferred over aquatic prey in forested headwater streams (Garman, 1991; Nakano, Fausch & Kitano 1999a; Nakano *et al.*, 1999b; Nakano, Miyasaka & Kuhara, 1999c; see review by Hunt, 1975). Thus, terrestrial invertebrates are an important seasonal resource to stream fishes (Cloe & Garman, 1996; Nakano *et al.*, 1999b,c). Moreover, the annual production of benthic invertebrates in headwater streams

may be insufficient to support *in situ* fish production (Allen's Paradox; Allen, 1951). More recent studies of production have suggested that such 'insufficiency' is partly offset by a subsidy of non-benthic food, i.e. terrestrial invertebrates (Waters, 1988, 1993). Accordingly, allochthonous food may be expected to represent an important energy source both seasonally and annually. Nevertheless, the annual contribution of terrestrial invertebrates to the energy budget of fish populations is still poorly understood.

In addition to seasonal differences, the riparian vegetation has been found to influence the input of terrestrial invertebrates (Mason & MacDonald, 1982; Garman, 1991; Cloe & Garman, 1996; Wipfli, 1997). The abundance and taxonomic composition of riparian invertebrates are largely influenced by the terrestrial vegetation (see Southwood, 1961; Schowalter, Webb & Crossley, 1981), which may thus determine the rate of supply of terrestrial invertebrates to stream channels (Cadawallader, Eden & Hook, 1980; Mason & MacDonald, 1982). Therefore, there could be great variation in the allochthonous inputs to fish diet among streams and even among reaches with different riparian vegetation. Although the need for a greater understanding of the significance of terrestrial invertebrate input for stream management has been recognized (Edwards & Huryn, 1996; Wipfli, 1997; Nakano *et al.*, 1999c), the annual contribution of terrestrial invertebrates to the energy budget of stream fish has never been compared among sites with differing riparian vegetation. In this study, we compared the annual input of terrestrial invertebrates and the contribution of that input to the prey consumption of salmonids in reaches of a Japanese headwater stream characterized by contrasting forest and grassland riparian vegetation.

## Methods

### *Study area*

The study was conducted in the middle reaches of the Horonai Stream that runs through the Tomakomai Experimental Forest of Hokkaido University (TOEF; 42°43'N, 141°36'E) in south-western Hokkaido, the northernmost island of the Japanese archipelago, from March 1995 to February 1996. This small, cold, spring-fed stream (14 km long, 2–5 m wide, <1%

**Table 1** Characteristics of habitat and fish in each study reach of the Horonai Stream

Variables	Riparian vegetation			
	Forest	Forest	Grass	Grass
Reach length (m)	52	42	46	43
Width (m)	2.9 ± 0.1 (20)	3.6 ± 0.1 (20)	3.3 ± 0.4 (20)	3.5 ± 0.3 (20)
Canopy shade (%)	94.3 ± 2.6 (20)	90.6 ± 2.8 (20)	30.1 ± 7.9 (20)	22.5 ± 7.8 (20)
Depth (cm)	17 ± 1 (20)	24 ± 1 (20)	18 ± 3 (20)	23 ± 1 (20)
Current velocity (ms <sup>-1</sup> )	0.46 ± 1 (20)	0.40 ± 1 (20)	0.42 ± 1 (20)	0.40 ± 1 (20)
Discharge (m <sup>3</sup> s <sup>-1</sup> )	0.24 ± 0.01 (8)	0.22 ± 0.01 (8)	0.21 ± 0.01 (8)	0.24 ± 0.01 (8)
Fish fork length* (cm)	14.1 ± 0.4 (113)	14.5 ± 0.3 (128)	12.2 ± 0.2 (122)	13.3 ± 0.3 (140)
Fish body mass* (g)	41.4 ± 4.0 (113)	47.6 ± 3.8 (128)	24.4 ± 1.9 (122)	33.1 ± 2.6 (140)

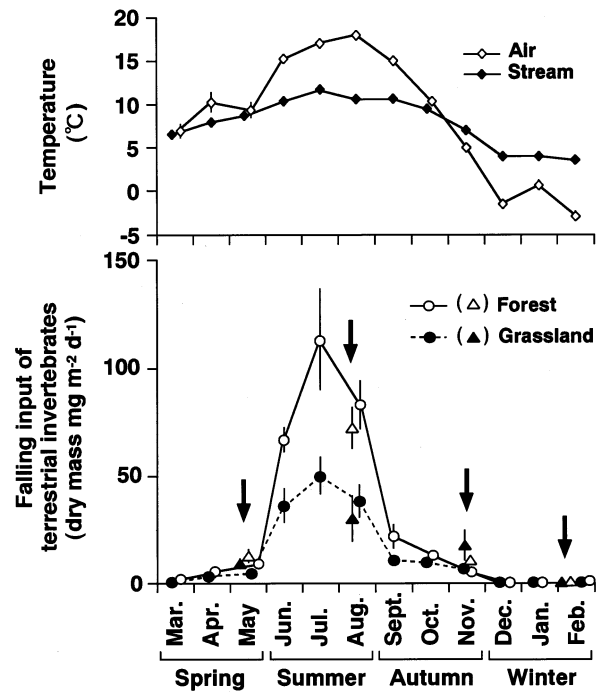
\* Fork length and body mass were obtained from each fish collected during the population estimates. Values are mean ± 1 SE. Numbers in parentheses denote sample sizes.

gradient) flows directly into the Pacific Ocean (see Urabe & Nakano, 1998). The discharge was relatively constant during the study period (ranging between 0.18 and 0.30 m<sup>3</sup> s<sup>-1</sup>). The stream catchment is primarily covered by cool-temperate deciduous forest, dominated by secondary-growth deciduous trees, e.g. oak *Quercus crispula* Blume, maple *Acer mono* Maxim, ash *Fraxinus mandshurica* Rupr and alder *Alnus hirsuta* Turcz, with an additional mixture of two grassland patches (c. 150 and 300 m in reach length, 100 and 200 m width, 1.5 and 6.0 ha area, respectively) and was mainly covered by exotic pasture (*Poa pratensis* L., *Dactylis glomerata* L. and *Phleum pratensis* L.). A few isolated stands of deciduous trees bordered the stream banks in the grassland patches. Most of the riparian trees in the catchment broke bud in late May and shed their leaves in mid-October.

Four study stretches (150 m<sup>2</sup> in surface area) were selected at random, two dominated by riparian forest and two by grassland (one in each of the two grassland patches). In the forest reaches, almost the entire stream channel was covered by the tree canopy, whereas the proportion of canopy shade was much lower in the grassland reaches (Table 1). However, other physical habitat attributes of the study reaches were similar. Monthly mean water temperatures varied from 3.1 to 11.8 °C during the study period, with the difference among the study reaches being within ± 2 °C in the same season (see Fig. 1). Annual mean air temperature and precipitation in 1994 were 6.3 °C and 1394 mm, respectively (Tomakomai Research Station, Hokkaido University, unpublished).

### Invertebrate sampling

To examine seasonal fluctuations in the input of terrestrial invertebrates by falling into the stream over a year (hereafter, 'falling input'), daily inputs were estimated from samples collected by pan traps set in each study reach for 7 days in each month during the



**Fig. 1** Monthly input by terrestrial invertebrates falling into the stream (mean ± 1 SE,  $n = 2$ ) in the forest and grassland reaches of the Horonai Stream, with monthly mean air and stream temperatures (mean ± 1 SE,  $n = 4$ ). Triangular symbols indicated by arrows show falling input of terrestrial invertebrates for two 24-h periods, at intervals of 5 or 6 days, in four seasons.

study period. Each pan trap ( $1 \times 1$  m area, 0.15 m depth) was coloured grey and supported on a stand. Five pan traps in each study reach were filled with water and two to three drops of surfactant, located c. 0.15 m above the water surface and randomly set along the length of each study reach. In addition, due to their design and location, the traps were not intended to measure the terrestrial invertebrates entering from the stream margins. The potential bias of the pan traps have been pointed out as acting as 'attracting traps' due to the surfactant used, which may have captured some specific taxa of insects (Southwood, 1966; Edwards & Hurn, 1995). However, this method has been widely used to quantify the terrestrial invertebrate input into the stream habitat (Mason & MacDonald, 1982; Cloe & Garman, 1996; Wipfli, 1997; Nakano *et al.*, 1999b,c). In winter (December–February), 40% ethylene glycol solution was used as antifreeze. Pan contents were sieved (through a 225- $\mu$ m mesh) every day and preserved in 5% buffered formalin solution until analysed.

In addition to the falling input, the in-stream input/output budget of terrestrial invertebrates was estimated for each study reach. Terrestrial invertebrates drifting into and out of the study reaches were surveyed for two 24-h periods, at intervals of 5 or 6 days, in each season: spring (May), summer (August), autumn (November) and winter (February). The 2-day sampling periods were conducted concurrently with the 7-day samples of falling input in each season (see Fig. 1). Stream drift was collected with 185- $\mu$ m mesh drift nets ( $0.25 \times 0.25$  m mouth opening, 1 m net length; Shiga-konchuu, Tokyo, Japan) at both the upstream and the downstream ends of each study reach. At each sampling site, four drift nets were placed across the stream for 20 min every 4 h (20, 24, 4, 8, 12 and 16 h) over a 24-h period, with their openings extending above the water surface to ensure that floating terrestrial invertebrates were captured. The water volume sampled was estimated from current velocity measured at the centre of each net opening using a portable current meter (Model CR-7, Cosmo-Riken Inc., Kashihara, Japan). Daily discharge was measured at the upstream end of each study reach after the drift survey using the U.S. Geological Survey mid-section method (Orth, 1983).

The biomass of benthic invertebrates was estimated from samples collected with a 225- $\mu$ m mesh Surber sampler ( $0.25 \times 0.25$  m in quadrat area, 1 m in net

length; Miura-Rika, Sapporo, Japan) at 12 locations selected at random in each study reach on the same days as the stream drift surveys in each season. Both the drift and the benthic samples were immediately preserved in 5% formalin solution.

### *Fish population and diet survey*

The abundance of salmonids in the study reaches was surveyed 2 days after the first drift survey in each season by the three-pass removal method, using a back-pack electrofishing unit (Model 12, Smith-Root Inc., Vancouver, WA, USA). Both ends of the reaches were blocked with 1-cm mesh seines during electrofishing. Fishes from each pass were anaesthetized using 2-amino-4-phenylthiazole hydrobromide, and their fork length (FL) and body mass (BM) measured in the field to the nearest 0.1 cm and 0.1 g, respectively (Table 1). Fish < 9 cm FL were excluded from the analysis because of their low capture rate (Y. Kawaguchi & S. Nakano, unpublished). Although four salmonid species—rainbow trout *Oncorhynchus mykiss* Walbaum, masu salmon *Oncorhynchus masou* Brevoort, white-spotted charr *Salvelinus leucomaenis* Pallas and Dolly Varden *Salvelinus malma* Walbaum—were captured in the study reaches, they were pooled for the present analyses because one species (rainbow trout) accounted for > 90% of the total fish biomass.

To estimate daily prey consumption, rainbow trout (> 9 cm FL) were collected by electrofishing (see above) every 4 h (20, 24, 4, 8, 12 and 16 h) over a 24-h period on the same days as the above stream drift surveys (i.e. 2 days in each season). The sampling reaches were established just downstream of each study reach to avoid disturbance (associated with electrofishing) to invertebrate drift and fish foraging in the study reaches. Diel foraging periodicity and diet composition of fish sampled for daily prey consumption was assumed to be identical to those in the study reaches immediately upstream, the adjacent stream reaches having the same riparian vegetation. Electrofishing proceeded upstream until six specimens had been captured (within a period of < 1 h), in each of the six sampling sessions per 24-h period, in each reach. Captured fish were transported to nearby facilities, anaesthetized and measured in the same way as for the population survey. The stomach contents were collected by stomach pumping with a

2-mL pipette to flush prey items from the stomach and preserved in 5% formalin solution until analysed (Giles, 1980). Captured fish were released at their original location at the end of the 24-h sampling period.

#### Sample analyses

Pan trap, benthos, drift and stomach content samples were all sieved once with a 225- $\mu$ m mesh to equalize the minimum size of invertebrates. They were then sorted into terrestrial and benthic invertebrates, and adult aquatic insects under a binocular microscope. Terrestrial invertebrates and adult aquatic insects were identified to order, and benthic invertebrates to family. Larvae and adults of terrestrial invertebrates were treated separately. Each invertebrate category was weighed (wet mass) to the nearest 0.01 mg after blotting for about 10 s, the error incurred for repeated measurements of wet mass being within  $\pm 6\%$  (S. Nakano, unpublished). Dry mass (after drying at 60 °C for 24 h) of random subsamples was measured to the nearest 0.01 mg for each category, and wet mass converted to dry mass according to regressions through the origin (range of slopes = 0.085–0.337,  $n = 7$ –30,  $r^2 = 0.71$ –0.99,  $P < 0.001$  for all 48 categories). For the analyses of all samples (except pan trap), benthic invertebrates and adult aquatic insects were pooled as 'aquatic invertebrates', because our primary focus was on terrestrial invertebrates as allochthonous prey. Adult aquatic insects were excluded from the analyses of the pan trap samples, owing to the primary focus being on terrestrial invertebrates as fish prey.

#### Data analysis

The daily input of terrestrial invertebrates falling into the study reaches measured using pan traps ( $\text{mg day}^{-1}$  per  $150 \text{ m}^2$ ) was estimated by multiplying the mean input for the five pan traps ( $\text{mg m}^{-2} \text{ day}^{-1}$ ) by the stream surface area ( $150 \text{ m}^2$ ). The drift biomass ( $\text{mg m}^{-3}$ ) was calculated by dividing the dry mass of invertebrates retained per net by the water volume sieved for each of the four nets in each sampling session (i.e. 24 net totals over a 24-h sampling period). Subsequently, both the drift input and output ( $\text{mg day}^{-1}$ ) were estimated for each study reach on each sampling day by multiplying the

mean value of the 24 drift biomass calculations by the daily stream discharge ( $\text{m}^3 \text{ day}^{-1}$ ).

Fish abundance was estimated using the maximum-likelihood generalized removal estimator (Otis *et al.*, 1978) via the computer program CAPTURE (White *et al.*, 1982). The biomass was estimated by multiplying the estimated fish abundance by the mean BM. Reach-based fish biomass was expressed as total biomass (mg) per  $150 \text{ m}^2$ .

The dry mass of prey invertebrates consumed by rainbow trout, the dominant salmonid, was estimated for each of the six 4-h sampling sessions (above), following Elliott & Persson (1978):

$$Ct = (St - So e^{-Rt})Rt / (1 - e^{-Rt}) \quad (1)$$

where  $C$  is the dry mass (mg) of prey consumed per 100 mg dry mass of fish in a sampling interval of  $t$  h,  $So$  and  $St$  are the mean dry masses of prey in the stomach per 100 mg dry mass of fish at the beginning and end of the interval, respectively,  $e$  is the exponent of natural logarithms and  $R$  is the rate of gastric evacuation. The dry mass of captured fish was estimated from the measured wet mass using a simple linear regression equation previously obtained (Y. Kawaguchi & S. Nakano, unpublished). Because the gastric evacuation rate of fish is generally influenced by water temperature, which fluctuated seasonally in the study stream, we measured the rate at four temperatures (2, 7, 9 and 12 °C) under laboratory conditions, following Elliott's (1972) method. The relationship between the estimated gastric evacuation rate ( $R$ ) and water temperature ( $T$ ) can be expressed as follows (Y. Kawaguchi & S. Nakano, unpublished):

$$R = e^{0.224T - 5.439} \quad (n = 4, r^2 = 0.95, P = 0.025) \quad (2)$$

Gastric evacuation rates to be used for estimation of daily prey consumption were obtained by substituting for stream temperature in the above equation (for each study reach on each sampling day). Gastric evacuation rate was assumed to be constant among the prey categories, following Elliott (1972) and the experimental findings over a 24-h period, during which temperature fluctuations were negligible. Finally, the daily prey consumption rate of rainbow trout was calculated separately for terrestrial and aquatic invertebrates, combining the prey consumption rate for the six 4-h sessions. This value was also converted into an area-based unit (i.e. area-based fish consumption;  $\text{mg day}^{-1}$  per  $150 \text{ m}^2$ ), taking the total

biomass of salmonids (dry mass) into consideration and assuming daily prey consumption to be equal among the four species.

The reach-based budget of terrestrial invertebrates was estimated from the data set of falling input, drift input, drift output and area-based fish consumption for each study reach on each sampling day. Although falling input was collected for 7 days each month, the values obtained over the 2-day sampling period, during which the other components of the budget were surveyed, were used for the estimation. Falling and drift input were summed to obtain total input, drift output and area-based fish consumption, thus providing total output, and the missing mass of terrestrial invertebrates (MMT) (e.g. those that fell on to the stream and reached the stream bank, or were deposited on the streambed, or were consumed by stream invertebrates, and/or were overcaptured by pan traps) estimated as (falling input + drift input) – (drift output + area-based fish consumption). In fact, overestimation of falling input has been reported in a previous study, which employed similar pan traps to those used here (Wipfli, 1997). The proportion of area-based fish consumption of terrestrial invertebrates was calculated as area-based fish consumption / (falling input + drift input).

We subsequently estimated the annual, reach-based budget of terrestrial invertebrates, assuming all of the above estimates on the actual sampling days to be constant over the remainder of each season. The periods from March to May, June to August, September to November and December to February were regarded as spring, summer, autumn and winter, respectively, because fluctuations in both the falling input of terrestrial invertebrates and stream temperature, at least, were relatively small within each of these periods (see Fig. 1).

#### Statistical analyses

For all statistical analyses, we considered study reaches as replicates. The falling inputs of terrestrial invertebrates were analysed with repeated measures two-way analysis of variance (ANOVAs), with vegetation types and season as the main factors and 7 sampling days within a season as a repeated (time) factor. The prey consumption rate of fishes was analysed with repeated measures three-way ANOVAs, with vegetation type, prey categories and

season as the main factors and 2 sampling days within a season as a repeated factor. In all of the repeated measures ANOVA tests, when significant between-subject effects were encountered, contrasts were performed as multiple comparison tests. The biomass of benthic invertebrates and fishes was analysed by two-way ANOVAs, with vegetation type and season as the main factors. When significant main factor effects were encountered, Scheffé tests were conducted as multiple comparison tests. An  $\alpha$  value of 0.05 was used for statistical significance, except for the multiple comparison tests for which an adjusted  $\alpha$  value was used according to the Bonferroni method (i.e.  $\alpha = 0.05/n$ , where  $n$  is the number of pairwise comparisons).

$\log_{10}(x + 1)$  transformations for exact values and arcsine-square-root transformations for percentage were conducted in order to standardize variances and improve normality, if necessary, to satisfy the assumptions for ANOVAs and  $t$ -tests. However, non-transformed data are presented unless otherwise stated.

## Results

### *Prey invertebrates*

In the Horonai Stream, seasonal fluctuations were apparent in the falling input of terrestrial invertebrates ( $\text{mg m}^{-2} \text{ day}^{-1}$ ) in both forest and grassland reaches, although the inputs differed considerably between them (Fig. 1). A repeated measures two-way ANOVA on the input revealed that both vegetation type and seasonal effects were significant, the interaction being non-significant (Table 2). None of the within-subject effects were significant in the analysis ( $P > 0.745$  for all). In this single year, the falling input of terrestrial invertebrates was relatively low in spring (March–May); thereafter, it increased dramatically and peaked in summer (June–August), decreased during autumn (September–November) and remained at minimum levels in winter (December–February) in both the forest and the grassland reaches. However, input in the forest was significantly greater than that in the grassland reaches, only from June to August ( $P < 0.011$  for all 3 months by contrast), there being no significant difference encountered over the remaining 9 months ( $P > 0.311$  for all). The annual falling input in the forest (mean  $\pm$

**Table 2** Results of repeated measures ANOVA for the effects of vegetation, season and invertebrate prey categories on the falling input of terrestrial invertebrates and daily fish consumption rate

Source	Falling input			Fish consumption rate		
	d.f.	F	P	d.f.	F	P
<i>Between-subjects</i>						
Vegetation	1	27.43	<0.001	1	0.98	0.338
Season	11	119.24	<0.001	3	29.59	<0.001
Category	—*	—	—	1	5.11	0.038
Vegetation × season	11	2.27	0.052	3	0.06	0.983
Vegetation × category	—	—	—	1	0.42	0.525
Season × category	—	—	—	3	17.83	<0.001
Vegetation × season × category	—	—	—	3	0.66	0.589
Error	24			16		

\* Invertebrate category factor not included in analysis of falling input.

Note that within-subjects effects, none of which was significant, have been omitted from this table.

1 SE =  $8.7 \times 10^3 \pm 0.3 \times 10^3 \text{ mg m}^{-2} \text{ year}^{-1}$ ) was 1.7 times greater than that in the grassland reaches ( $5.1 \times 10^3 \pm 0.8 \times 10^3 \text{ mg m}^{-2} \text{ year}^{-1}$ ), the summer input contributing 76% of the total in the former and 54% of the total in the latter.

The biomass of benthic invertebrates ( $\text{mg m}^{-2}$ ) in the grassland reaches was greater than that in the forest reaches, although no seasonal changes were found using a two-way ANOVA (Fig. 2). There was a significant vegetation effect ( $F_{1,8} = 9.79$ ,  $P = 0.014$ ), but no seasonal ( $F_{3,8} = 1.29$ ,  $P = 0.344$ ) or interaction effects ( $F_{3,8} = 0.57$ ,  $P = 0.649$ ).

#### Fish population and diet

Overall means of both FL ( $15.0 \pm 0.1$  [1 SE] cm, range = 9.0–26.6) and BM ( $47.4 \pm 1.0$  [1 SE] g, range 9.6–224.7) of the fish ( $n = 768$ ) captured for the dietary analyses did not differ significantly from those of the fish captured in the population survey (FL,  $t = -0.044$ , d.f. = 1653,  $P = 0.964$ ; BM,  $t = 0.278$ , d.f. = 1653,  $P = 0.782$ , by unpaired  $t$ -tests for  $\log_{10}$  transformed data; see Table 1). Fish biomass ( $\text{mg per } 150 \text{ m}^{-2}$ ) in the forest reaches was significantly greater than that in the grassland reaches (two-way ANOVA;  $F_{1,8} = 71.86$ ,  $P < 0.001$ ) and also varied significantly among seasons ( $F_{3,8} = 13.10$ ,  $P = 0.002$ ), with a non-significant interaction effect ( $F_{3,8} = 2.44$ ,  $P = 0.139$ ; Fig. 3). Fish biomass in autumn was similar to that in summer ( $P = 0.142$  by Scheffé test) but was greater than that in spring ( $P = 0.006$ ) and winter ( $P = 0.004$ ), both of the latter also being similar to that in summer ( $P > 0.120$  for both).

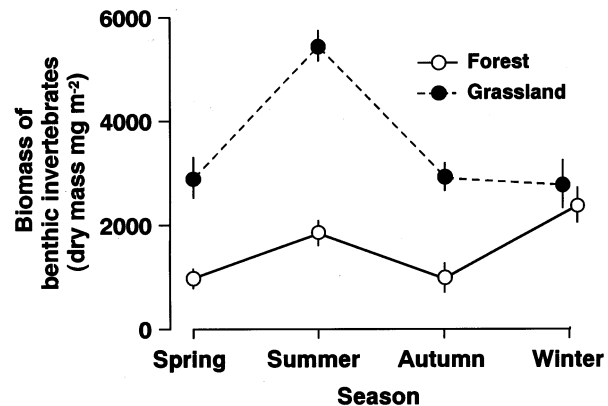


Fig. 2 Seasonal changes in biomass (mean  $\pm 1$  SE,  $n = 2$ ) of benthic invertebrates in the forest and grassland reaches of the Horonai Stream.

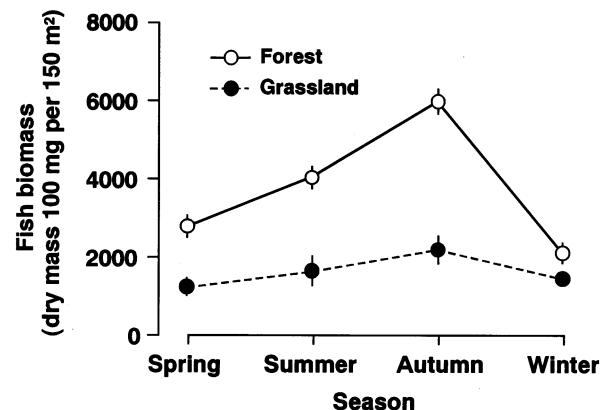


Fig. 3 Seasonal changes in fish biomass (mean  $\pm 1$  SE,  $n = 2$ ) in the forest and grassland reaches of the Horonai Stream.

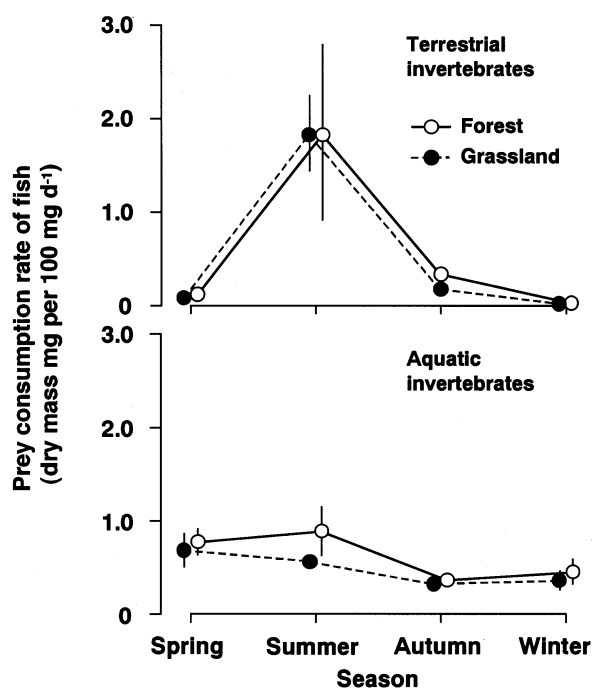


Fig. 4 Seasonal changes in consumption rates (mean  $\pm$  1 SE,  $n = 2$ ) on terrestrial and aquatic invertebrates by rainbow trout in the forest and grassland reaches of the Horonai Stream.

The prey consumption rates of fish (mg per 100 mg day<sup>-1</sup>) of either terrestrial or aquatic invertebrates did not differ between vegetation types, although they changed dramatically with season (Fig. 4). The repeated measures three-way ANOVA revealed that the consumption rate differed significantly both among seasons and prey categories, with a non-significant vegetation effect (Table 2). Of the

interactions, only season by prey category was significant. None of the within-subject effects were significant in the analysis ( $P > 0.347$  for all). The consumption rate of terrestrial invertebrates in summer was much greater than that in any other season ( $P < 0.001$  for all by contrast; Fig. 4), there being no difference among spring, autumn and winter ( $P > 0.051$  for all combinations). The contribution of terrestrial invertebrates to daily prey consumption in the forest and grassland reaches was *c.* 11 and 7% in spring, 68 and 77% in summer, 48 and 33% in autumn, and 1 and 1% in winter, respectively. The consumption rates of aquatic invertebrates in summer and spring were greater than those in autumn and winter ( $P < 0.045$  for all combinations), those for summer and spring being similar ( $P = 0.059$ ), and autumn and winter being likewise ( $P = 0.722$ ). In contrast to summer, when the consumption rate of terrestrial invertebrates was greater than aquatic invertebrates ( $P < 0.001$ ), the rate of aquatic invertebrate consumption was greater in both spring ( $P < 0.001$ ) and winter ( $P = 0.004$ ). The consumption rate, however, was similar between the two prey categories in autumn ( $P > 0.398$ ). Taking such seasonal changes in both prey consumption rate and biomass into consideration, terrestrial invertebrates were estimated as having contributed 49% (mean  $\pm$  1 SE =  $5.3 \times 10^3 \pm 0.4 \times 10^3$  mg m<sup>-2</sup> year<sup>-1</sup>) of the annual, area-based total prey consumption ( $10.9 \times 10^3 \pm 1.7 \times 10^3$  mg m<sup>-2</sup> year<sup>-1</sup>) in the forest and 53% ( $2.0 \times 10^3 \pm 0.3 \times 10^3$  mg m<sup>-2</sup> year<sup>-1</sup>) of the total ( $3.8 \times 10^3 \pm 0.6 \times 10^3$  mg m<sup>-2</sup> year<sup>-1</sup>) in the grassland reaches, with annual, area-based consumption in the former being

Table 3 Reach-based budget of terrestrial invertebrates (dry mass mg day<sup>-1</sup> per 150 m<sup>2</sup>; mean  $\pm$  1 SE,  $n = 2$ ) in the forest and grassland reaches of the Horonai Stream in each season

Vegetation type	Season	Daily input		Daily output		
		Falling input	Drift input	Area-based fish consumption	Drift output	MMT
Forest	Spring	1850 $\pm$ 430 (92.7)	150 $\pm$ 20 (7.3)	330 $\pm$ 210 (16.5)	370 $\pm$ 190 (18.5)	1300 (65.0)
	Summer	10 770 $\pm$ 1420 (86.2)	1720 $\pm$ 830 (13.8)	6590 $\pm$ 2580 (52.8)	2110 $\pm$ 750 (16.9)	3790 (30.3)
	Autumn	1600 $\pm$ 310 (68.3)	740 $\pm$ 170 (31.7)	1680 $\pm$ 120 (71.8)	580 $\pm$ 150 (24.8)	80 (3.4)
	Winter	30 $\pm$ 10 (14.6)	170 $\pm$ 90 (85.4)	10 $\pm$ 10 (5.0)	170 $\pm$ 90 (85.0)	20 (10.0)
Grass	Spring	1300 $\pm$ 340 (93.9)	80 $\pm$ 60 (6.1)	50 $\pm$ 10 (3.7)	280 $\pm$ 150 (20.1)	1050 (76.2)
	Summer	4480 $\pm$ 1560 (91.6)	410 $\pm$ 60 (8.4)	2790 $\pm$ 310 (57.1)	400 $\pm$ 20 (8.2)	1700 (34.7)
	Autumn	2610 $\pm$ 1020 (87.9)	360 $\pm$ 220 (12.1)	400 $\pm$ 180 (13.5)	250 $\pm$ 210 (8.5)	2320 (78.0)
	Winter	10 $\pm$ 10 (25.4)	40 $\pm$ 30 (74.6)	4 $\pm$ 2 (8.0)	40 $\pm$ 40 (80.0)	6 (12.0)

Percentages given in parentheses. MMT stands for the missing mass of terrestrial invertebrates.



2.7 times greater than that in the latter. Summer area-based consumption of terrestrial invertebrates contributed 77 and 86% of the annual consumption on the former in the forest and grassland reaches, respectively.

#### *Reach-based budget*

In both the forest and the grassland reaches, a clear seasonal change was found in each component—falling and drift input, area-based fish consumption, drift output and missing mass—of the reach-based terrestrial invertebrate budget (Table 3). The contribution of falling input to the total daily input was much greater than that of drift input in all but the winter season, when the trend was reversed, in both forest and grassland reaches. Area-based fish consumption in the forest, however, was greater than that in the grassland reaches throughout the year, although seasonal fluctuations were observed in both vegetation types (Table 3). A relatively high proportion of the daily input was consumed in-stream during both summer and autumn in the forest, but in summer only in the grassland reaches. The contribution of drift output to the total daily output was much smaller than that of area-based fish consumption in all but the winter season. The proportion of MMT was relatively high in spring, compared with other seasons, in the forest reaches, and in spring and autumn in the grassland reaches.

The annual reach-based, total input of terrestrial invertebrates was estimated to be  $1564 \times 10^3$  mg per  $150 \text{ m}^2$  in the forest and  $852 \times 10^3$  mg per  $150 \text{ m}^2$  in the grassland reaches, being 1.8 times greater in the former (Fig. 5). The contribution of falling input to the annual, total input (84% in the forest and 90% in the grassland reaches) was much greater than that of drift input, which almost equalled drift output in all of the reaches studied. The proportion of area-based fish consumption of the annual, total input to the forest reaches (51%) was greater than that in the grassland reaches (35%), whereas the MMT proportion of the annual, total input was estimated to be 30 and 55% in the forest and grassland reaches, respectively.

#### **Discussion**

In the Horonai Stream, the annual biomass of terrestrial invertebrates falling into the forest reaches

(mean  $\pm 1$  SE,  $8.7 \times 10^3 \pm 0.3 \times 10^3 \text{ mg m}^{-2} \text{ year}^{-1}$ ) was 1.7 times greater than that in grassland reaches ( $5.1 \times 10^3 \pm 0.8 \times 10^3 \text{ mg m}^{-2} \text{ year}^{-1}$ ). Invertebrate input differed between the vegetation types only in summer, however, when it reached a peak in both the forest (contributing 76% of the annual input) and grassland reaches (54%). The seasonal dynamics of terrestrial input may simply be associated with greater invertebrate biomass and acting in summer periods (S. Nakano, unpublished). When converted to equivalent units, the mean daily input of terrestrial invertebrates in the forest reaches of this stream in summer was comparable with those reported in previous studies of other headwater streams in cool-temperate deciduous forests, whereas the value for the grassland reaches was much lower (Mason & MacDonald, 1982; Cloe & Garman, 1996). The spatial structure of riparian vegetation has been considered as a primary factor influencing the summer input of terrestrial invertebrates (Edwards & Huryn, 1996; Nagasaka, Yanai & Sato, 1996; Wipfli, 1997). For instance, Edwards & Huryn (1996) showed that the input of terrestrial invertebrates to grassland streams in summer was less than that to native forested streams in New Zealand, and attributed this difference to greater canopy cover in the latter. Even within forested streams, the input of terrestrial invertebrates in headwaters (i.e. low-order), heavily shaded narrow stream channels, was greater than that in wider reaches downstream (Cloe & Garman, 1996). In the Horonai Stream, over 90% of the entire stream channel was covered by tree canopy in the forest reaches, whereas canopy cover was only 20–30% in the grassland reaches. Although the two grassland patches associated with the Horonai Stream were quite small (1.5 and 6 ha area), such variations in riparian vegetation could be important determinants of terrestrial inputs to streams. Well-developed overhanging vegetation in the forest reaches should enhance the summer input of invertebrates with little or no flying ability (e.g. Lepidoptera larvae, coleopterans and spiders; see Appendix 1), although the potential difference in invertebrate biomass between the two vegetation types in the study area is still unknown.

The consumption of terrestrial invertebrates by salmonids was very high in summer in both the forest (contributing 77% of the annual consumption

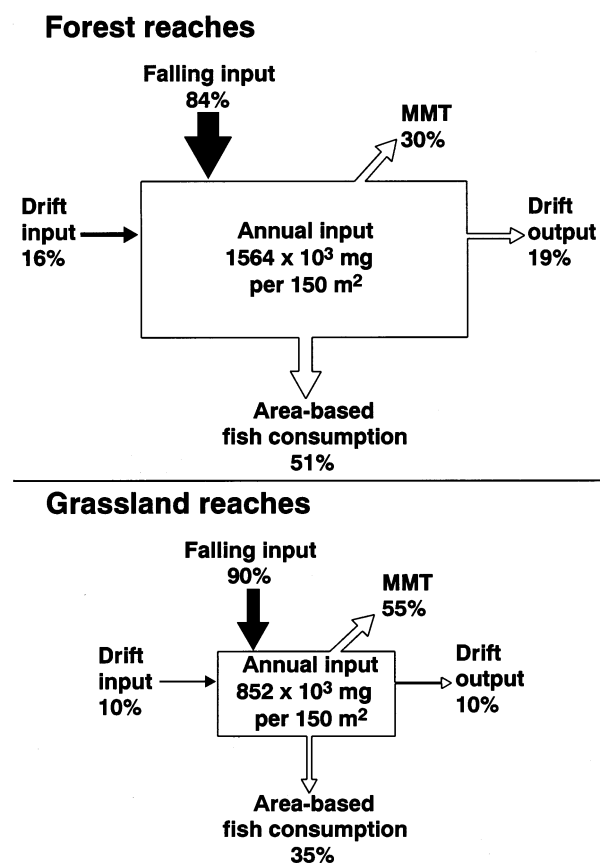


Fig. 5 Annual reach-based budget of terrestrial invertebrates in the forest and grassland reaches of the Horonai Stream. Arrow thickness indicates proportion of each component (black arrows: input to; white arrows: output from the study reaches). MMT stands for the missing mass of terrestrial invertebrates.

of the former) and the grassland reaches (86%). Irrespective of vegetation types, terrestrial invertebrates were the primary prey of the fish in summer, comprising 68 and 77% of daily prey consumption in the forest and grassland reaches, respectively. Terrestrial invertebrates have been considered as an especially important seasonal subsidy for salmonids during summer, partly explained by the minimum in benthic invertebrates biomass at that time (Hynes, 1970; Cloe & Garman, 1996). However, in the study, intensive exploitation of terrestrial invertebrates could only be explained by their great input to the stream and selective foraging by fish in summer, benthic invertebrate biomass being no less than in other seasons in the Horonai Stream. Nakano *et al.* (1999b) showed that, in summer, the total falling input and drift biomass of terrestrial invertebrates in the Horonai

Stream, and the prey consumption rate by rainbow trout during the day, were much greater than their equivalents during the night (see Edwards & Huryn, 1995). In contrast, the fact that most aquatic invertebrates enter stream drift at night when salmonids are inactive has been reported for many streams (Waters, 1972; Allan, 1995; see also Miyasaka & Nakano, 1999 for the Horonai Stream). In addition, the individual mean size of terrestrial invertebrates is much greater than that of aquatic invertebrates in the Horonai Stream (Nakano *et al.*, 1999b). It is also known that drift feeding fishes preferentially select large prey (Edwards & Huryn, 1996). Nakano *et al.* (1999b) concluded that differences in both the timing of supplies and prey size between the prey categories were the primary factors behind the selective foraging by rainbow trout on terrestrial invertebrates. Moreover, because both the basal and the active metabolic rates of fish generally increase with water temperature (Brett & Groves, 1979), the daily prey consumption of salmonids in summer, when water temperature is relatively high, is greater than in other seasons.

In the Horonai Stream, the annual area-based fish consumption of terrestrial invertebrates in the forest ( $5.3 \times 10^3 \text{ mg m}^{-2} \text{ year}^{-1}$ ; 51% of the annual, total input) was 2.7 times greater than that in the grassland reaches ( $2.0 \times 10^3 \text{ mg m}^{-2} \text{ year}^{-1}$ ; 35%), the annual, total input in the former being 1.8 times greater than that in the latter. However, the difference in both the daily terrestrial invertebrate input and the area-based fish consumption resulted in great variations in the proportion of each reach-based budgetary value to the total input among seasons and between vegetation types. In summer, the proportion of area-based fish consumption attributable to total terrestrial invertebrate input was relatively high, being similar between the forest and the grassland reaches regardless of the different daily inputs between the vegetation types. Although the total input of terrestrial invertebrates in the forest was much greater than that in the grassland reaches, fish in the latter achieved a consumption rate nearly equal to that of fish in the forested reaches. This was probably related to the smaller fish biomass in the grassland reaches. In the other seasons, the proportion of area-based fish consumption to the total input was generally low, due to the low daily prey consumption rate of fish (with the exception of the autumn value for the forest reaches,

when fish consumed about 72% of the relatively small input). At that time, fish biomass reached the maximum recorded in the forest reaches, due to the recruitment of underyearling fry into the size class ( $> 9$  cm) examined here (Y. Kawaguchi & S. Nakano, unpublished). This resulted in relatively high area-based fish consumption, although the daily consumption rate of terrestrial invertebrates in autumn was much lower than in summer. In both vegetation types, invertebrates falling in contributed much more to the total input than drift in all seasons other than winter. The situation was reversed in winter, when prey consumption by fish was at a minimum. Edwards & Huryn (1995), who estimated that c. 5% of annual trout production was supported by terrestrial invertebrates in a New Zealand stream, assumed that trout consumed all of the food input. The present study, however, suggests that even though the above estimated value is a tenth of that obtained for the Horonai Stream, the assumption of total consumption of terrestrial prey is liberal, considering the area-based fish consumption rate obtained in the present study.

A relatively high proportion of the daily input was regarded as missing mass of terrestrial invertebrates in spring in both the forest and the grassland reaches, and also in autumn in the latter. In all of these, dipterans contributed 40% or more of the total falling input (Appendix 1). Because pan traps attract Diptera (Southwood, 1966; Power, 1985; Edwards & Huryn, 1996), there exists a potential for the falling input of terrestrial invertebrates to be overestimated, especially if the input is dominated by flies. Although, to date, no studies have attempted to assess actual area-based fish consumption of terrestrial invertebrates by fish (but see Townsend & Hildrew, 1979; Lancaster & Robertson, 1995), a previous study has estimated the reach-based, in-stream retention of the latter, based on the difference between the total (i.e. falling and drift) input and drift output (Cloe & Garman, 1996). However, because they employed pan traps similar to those used in the present study, such retention, considered as actual fish consumption, may have been overestimated.

In this study, the contribution of terrestrial invertebrates to the annual, total prey consumption of stream salmonids was estimated as being nearly equal (about 50%) between the forest and the grass-

land reaches. Fish biomass in the latter, however, was less than that in the forest reaches, where greater terrestrial invertebrate inputs but smaller benthic invertebrate biomass were recorded. In addition, drift input almost equalled drift output in both vegetation types, suggesting that in-stream retention (i.e. consumption plus missing mass of terrestrial invertebrates) almost balanced the falling input. In reaches of the Horonai Stream where terrestrial invertebrate input was experimentally reduced using a greenhouse-type cover (see figure 1 of Nakano *et al.*, 1999c), the emigration of salmonids increased dramatically, resulting in a smaller summer biomass than in adjacent unmanipulated reaches (Y. Kawaguchi & S. Nakano, unpublished). Their experimental study suggested a potential for the local distribution of stream salmonids to be controlled partly by the heterogeneous supplies of allochthonous, terrestrial prey from riparian canopies. Contrasting terrestrial invertebrate inputs, but not benthic invertebrate biomass, from differing riparian vegetation types may underlie the observed differences in salmonid biomass, and may interact in complex ways with other abiotic factors, such as physical habitat structure (Inoue, Nakano & Nakamura, 1997; Inoue & Nakano, 1998; see Urabe & Nakano, 1998, 1999 for the Horonai Stream). Moreover, Nakano *et al.* (1999c) showed that fish predation pressure in the Horonai Stream shifted dramatically from terrestrial to benthic invertebrates when the input of the former was reduced experimentally. Consequently, the ensuing depletion of herbivorous aquatic invertebrates resulted in an increase in periphyton biomass. Riparian vegetation regimes which promote heterogeneous inputs of allochthonous prey can play an important role in determining the spatial distribution and dynamics of stream fish populations by 'bottom-up' control, and also the dynamics of benthic communities through the alteration of 'top-down' forces in stream food webs.

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**Appendix 1: Seasonal changes in taxonomic composition (dry mass  $\text{mg m}^{-2} \text{day}^{-1}$ ) of falling input of terrestrial invertebrates in the forest and grassland reaches of the Horonai Stream**

Vegetation type	Taxa	Spring	Summer	Autumn	Winter
Forest	Coleoptera	2.32 (32.8)	28.73 (33.2)	0.62 (4.1)	0.01 (2.0)
	Diptera	2.95 (41.7)	19.20 (22.2)	3.46 (22.7)	0.02 (4.0)
	Hymenoptera	0.24 (3.4)	4.62 (5.3)	1.66 (10.9)	0.00 (0.0)
	Lepidoptera (L <sup>a</sup> )	0.01 (0.1)	11.14 (12.9)	0.75 (4.9)	0.00 (0.0)
	Lepidoptera (A <sup>b</sup> )	1.07 (15.1)	10.03 (11.6)	1.78 (11.6)	0.37 (74.0)
	Hemiptera	0.13 (1.9)	2.25 (2.6)	2.09 (13.7)	0.01 (2.0)
	Collembola	0.01 (0.1)	0.21 (0.2)	0.04 (0.3)	0.05 (10.0)
	Spider	0.35 (4.9)	8.14 (9.4)	3.21 (21.0)	0.04 (8.0)
	Others	0.00 (0.0)	2.28 (2.6)	1.65 (10.8)	0.00 (0.0)
Grass	Coleoptera	0.58 (14.7)	4.34 (10.8)	0.03 (0.4)	0.00 (0.0)
	Diptera	1.83 (46.6)	11.45 (28.4)	4.26 (48.3)	0.05 (38.5)
	Hymenoptera	0.29 (7.5)	4.13 (10.3)	0.91 (10.4)	0.00 (0.0)
	Lepidoptera (L <sup>a</sup> )	0.00 (0.0)	8.99 (22.3)	0.12 (1.3)	0.00 (0.0)
	Lepidoptera (A <sup>b</sup> )	0.81 (20.7)	7.27 (18.0)	1.41 (16.0)	0.02 (15.4)
	Hemiptera	0.04 (1.0)	1.52 (3.8)	1.17 (13.3)	0.01 (7.7)
	Collembola	0.03 (0.9)	0.00 (0.0)	0.00 (0.0)	0.01 (7.7)
	Spider	0.34 (8.6)	1.40 (3.5)	0.89 (10.1)	0.04 (30.8)
	Others	0.00 (0.0)	1.16 (2.9)	0.02 (0.2)	0.00 (0.0)

a, Larva; b, Adult.

Percentages given in parentheses.