Ecology Letters, (2002) **5**: 333–337

REPORT

Indirect effect of aquatic insect emergence on a terrestrial insect population through by birds predation

Masashi Murakami[1]* and Shigeru Nakano[2]†
[1]*Tomakomai Research Station, Hokkaido University Forests, Takaoka, Tomakomai, 053–0035, Japan, and* [2]*Center for Ecological Research, Kyoto University, Hirano-cho, Kamitanakami, Otsu, 520–2113, Japan.*
**Correspondence: Masashi Murakami. E-mail: masa@exfor.agr.hokudai.ac.jp*
†Deceased.

Abstract

A manipulative field experiment was performed to determine the effect of birds, subsidized by aquatic insect emergence, on the insect herbivores in a riparian deciduous forest. Insectivorous birds were observed more frequently in the riparian forest than in upland forest away from the stream, utilizing both herbivorous insects feeding on the riparian vegetation and aquatic insects emerging from the stream as their prey. Field experiments revealed that the insect herbivore population in the riparian forest was more depressed by bird predation than that in the upland forest. This suggests that allochthonous prey input to the *in situ* prey population was responsible for a modification in the interaction between birds and herbivorous insects, resulting in a heterogeneous food web structure in the forest.

Keywords

Aquatic insect emergence, forest bird, forest–stream ecotone, leaf roller, Lepidoptera.

Ecology Letters (2002) 5: 333–337

INTRODUCTION

Most ecosystems comprise a mosaic of heterogeneous habitats differing in environmental properties. The movements of nutrients, detritus and organisms across these habitats are important because they often exceed internal factors and alter the dynamics and structure of the communities involved (Polis *et al.* 1996, 1997). However, such allochthonous effects occur mainly in a spatially heterogeneous manner. At the boundary between habitats, such effects are maximized.

The spatial aspects of food webs are essential for an understanding of community structure and dynamics (Holt 1977, 1996). In most systems the pattern of resource distribution is heterogeneous, resulting in a heterogeneous distribution of predators, most of which utilize a variety of prey types simultaneously. When the distributional patterns of two prey species differ and the distribution of predators is determined by the first prey species, predation intensity on the second prey species can be indirectly affected by the distribution of the first. These phenomena suggest a heterogeneous occurrence of indirect interactions between prey species sharing a common predator.

In a forest–stream ecotone, the forest birds depend highly upon aquatic insects emerging from the stream early in spring, the distribution of the former tending strongly towards the stream (Nakano & Murakami 2001). Before spring leafing, the terrestrial productivity in a temperate deciduous forest is almost zero. In contrast, stream productivity within a temperate deciduous forest is highest during the forest defoliation period, as the streams become more exposed to sunlight (Sumner & Fisher 1979) and experience relatively high water temperatures (Nakano & Murakami 2001). Such asynchrony in productivity between the forest and stream ecosystems is responsible for a significant seasonal energy flow from the stream to the forest.

Many studies have demonstrated the occurrence of top-down control of herbivorous insects by birds (Holmes *et al.* 1979; Murakami & Nakano 2000). Murakami (1999), for example, showed that a population of leaf rolling Lepidoptera larvae on Japanese lilac (*Syringa reticulata*) was controlled by bird predation. Because Japanese lilacs break bud earlier than other tree species in the forest area studied, the foraging activity of insectivorous birds was concentrated on the herbivores on the former tree species during early spring.

Considering these phenomena, we hypothesized that an emerged aquatic insect subsidy supports a denser bird population along a stream compared with that in an adjacent upland forest, resulting in depression of the herbivore population on riparian vegetation in early spring (just after budbreak). Accordingly, this study analysed the distribution and abundance of birds in a riparian and upland forest and assessed the degree by which forest birds are subsidized by emerged aquatic insects. We also addressed the manner in which the aquatic subsidies affect bird distribution within a forest, and hence the herbivore population.

METHODS

Study area and materials

Field studies were conducted in the forest along the Horonai Stream in the Tomakomai Experimental Forest (TOEF; 42°43′ N, 141°36′ E), Hokkaido, Japan, during a 26-day period in May and June 1999. The forest was dominated by deciduous tree species, including oak (*Quercus crispula*), cherry (*Prunus sargentii*) and ash (*Fraxinus mandshurica*), plus 30 other canopy species, with Japanese lilac dominating the shrub layer (1–3 m in height). The tree species composition and densities of riparian and upland forest were similar, with no clear boundary existing between these forest types. Six plots (20 × 50 m) were established, three immediately adjacent to the stream (riparian) and three in upland forest 200 m distance from the stream. Each plot was separated from adjacent plots by at least 500 m. Inside each plot, bird observations, insect monitoring and bird exclusion experiments were conducted. In both forest types, most tree species break bud in mid-May and shed their leaves in mid-October. During the experiment, lilacs broke bud on 3 May, at which time Lepidoptera leaf rollers hatched. There were no significant differences in water content or leaf toughness between riparian and upland lilac trees measured on 6 June (water content: 66.9 ± 1.2 (SE) % for riparian, 65.9 ± 1.9 for upland; $n = 10$ for each, one-way ANOVA, $F = 1.965$, d.f. = 1,18, $P = 0.178$; leaf toughness: 164.3 ± 7.6 mg cm^3 for riparian, 166.1 ± 6.4 for upland; $n = 10$ for each, one-way ANOVA, $F = 0.328$, d.f. = 1,18, $P = 0.574$; see Murakami 1997).

The four dominant insectivorous bird species in the overall forest were great tits (*Parus major*), marsh tits (*Parus palustris*), the narcissus flycatchers (*Ficedula narcissina*) and the crowned willow warblers (*Phylloscopus occipitalis*). Three dominant leaf rollers occurred on the lilac: *Homonopsis foederatana*, *Archips viola* and *Zeiraphera corpulentana* (Murakami 1999).

Bird observations

The visiting frequencies to each plot and prey types for the four dominant bird species were recorded every other day from 21 May to 8 June 1999, a total of 10 days. Because narcissus flycatchers were not recorded as utilizing leaf rollers on lilac trees throughout the study period, this species was excluded from further consideration. Each day, three plots were observed for 1 h, resulting in each plot having been observed for 5 h during the study period. The visiting frequency of the birds was expressed as the number of bird visits per an hour (visitation rate). Differences in the visitation rate were compared between riparian and upland forests (one-way ANOVA) separately for each bird species. The foraging behaviour of each bird species was also observed, one individual of each being selected and observed for 5 min at each plot during each observation period. Prey types, which were classified as leaf rollers, other terrestrial prey and aquatic prey, were identifiable on 551 (81.1%) out of a total of 679 observations.

Arthropod sampling

The abundance of flying insects was surveyed by a malaise trap (Townes 1972). In each of the six plots, one trap was set during 1–8 June 1999 (middle of the study period). Collected arthropods were preserved in 70% ethanol and sorted into terrestrial and aquatic insects, component species being identified to order. For Diptera, the samples were further identified to family for subsequent separation between terrestrial and aquatic forms. The biomass of each order and family was measured as wet mass (nearest to 0.1 mg) and the dry mass was estimated subsequently (see Nakano *et al.* 1999a). The insect masses were compared between riparian and upland forests (one-way ANOVA) separately for terrestrial and aquatic insects.

Bird exclusion experiment

On 17 and 18 May, five randomly selected lilac trees in each of the three riparian and three upland plots (30 trees total) were enclosed by cages of 15-mm nylon mesh net that allowed most insects but no birds to pass through. An additional 30 non-enclosed trees, 15 from riparian and 15 from upland plots, were selected as controls. Light attenuation by the net was 1.5%. The number of three dominant leaf roller species per shoot was calculated at the end of the experiment (10 and 11 June) by counting the numbers of leaf rolls and shoots on each individual tree. A two-way ANOVA was used to detect the effects of bird removal on the number of leaf rollers, treatment and site (riparian or upland) being the factors.

When necessary, exact values were log10 transformed to standardize variances and improve normality (Sokal & Rohlf 1995). All statistical tests were two-tailed. For all tests, an alpha value of 0.05 was used for statistical significance.

RESULTS

Bird observation

Bird visitation rates to the riparian plots were lower than those to the upland forest plots for great tits ($F = 11.60$, d.f. = 1,4, $P = 0.027$) and crowned willow warblers ($F = 9.02$, d.f. = 1,4, $P = 0.040$; Fig. 1), with no significant difference being found in visitation rates for marsh tits ($F = 0.454$, d.f. = 1,4, $P = 0.537$). In the riparian plots, all three bird species frequently utilized aquatic insects emerging from the stream (Fig. 2, 30–60% for each bird species). Leaf rollers were also utilized by the three bird species (at a rate of 15–50%). In the upland forest the birds rarely utilized aquatic insects dispersed from stream, taking leaf rollers (Fig. 2, 30–45%) and other terrestrial insects. Although the rate of leaf roller utilization in the riparian forest was less than that in the upland forest, the amount of overall predation on leaf rollers was much higher in the riparian forest because of the greater bird population and therefore greater visitation frequency (Fig. 2).

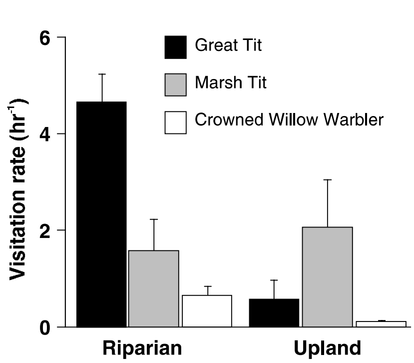

Figure 1 Comparison of the hourly foraging visitation numbers to a lilac tree in riparian and upland forest. Vertical bars indicate standard errors.

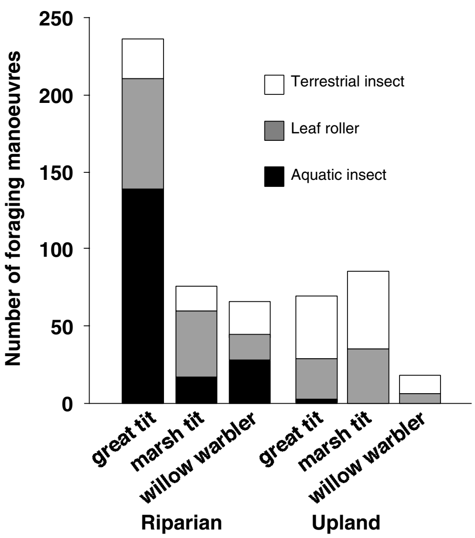

Figure 2 Numbers of foraging manoeuvres for each prey type for three dominant bird species.

Coal tits (*Parus ater*: nine occasions) and pale-legged willow warblers (*Phylloscopus tenellipes*: three occasions) were the only other bird species that visited the lilac trees and foraged on leaf rollers during the observation period.

Aquatic and terrestrial prey

No significant difference occurred in terrestrial prey biomass between the riparian and upland forests ($F = 0.65$, d.f. = 1,4, $P = 0.786$; one-way ANOVA), whereas aquatic prey biomass was much higher in the former ($F = 18.59$, d.f. = 1,4, $P = 0.013$, Fig. 3).

Bird exclusion experiment

The impacts of birds differed among the leaf roller species. *H. foederatana* numbers decreased due to bird predation, particularly in the riparian forest plots, as shown by the significant effects of both treatment ($F = 21.03$, d.f. = 1,36, $P < 0.001$) and site ($F = 8.16$, d.f. = 1,36, $P = 0.007$; two-way ANOVA; Fig. 4), with an interaction also being significant ($F = 4.47$, d.f. = 1,36, $P = 0.042$). No significant bird effects were found on *A. viola* (treatment: $F = 0.001$, d.f. = 1,36, $P = 0.974$; site: $F = 1.324$, d.f. = 1,36, $P = 0.257$; interaction: $F = 0.058$, d.f. = 1,36, $P = 0.811$) or *Z. corpulentana* leaf roller numbers (treatment: $F = 0.086$, d.f. = 1,36, $P = 0.772$; site: $F = 0.035$, d.f. = 1,36, $P = 0.852$; interaction: $F = 0.47$, d.f. = 1,36, $P = 0.497$), indicating that the latter two species were not utilized by birds.

DISCUSSION

Whereas the great tits and crowned willow warblers were subsidized by aquatic insects emerging from the stream, marsh tits were not affected by aquatic insect emergence. Differences in foraging tactics among bird species can effect

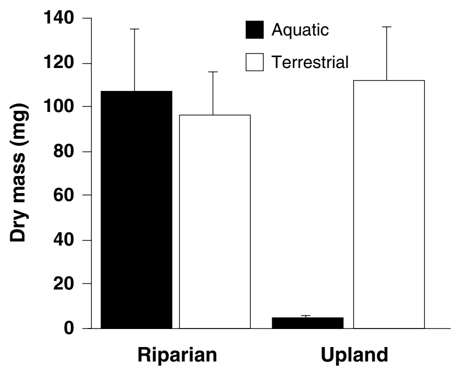

Figure 3 Biomass of aquatic and terrestrial insects in riparian and upland forests caught by malaise trap. Vertical bars indicate standard errors.

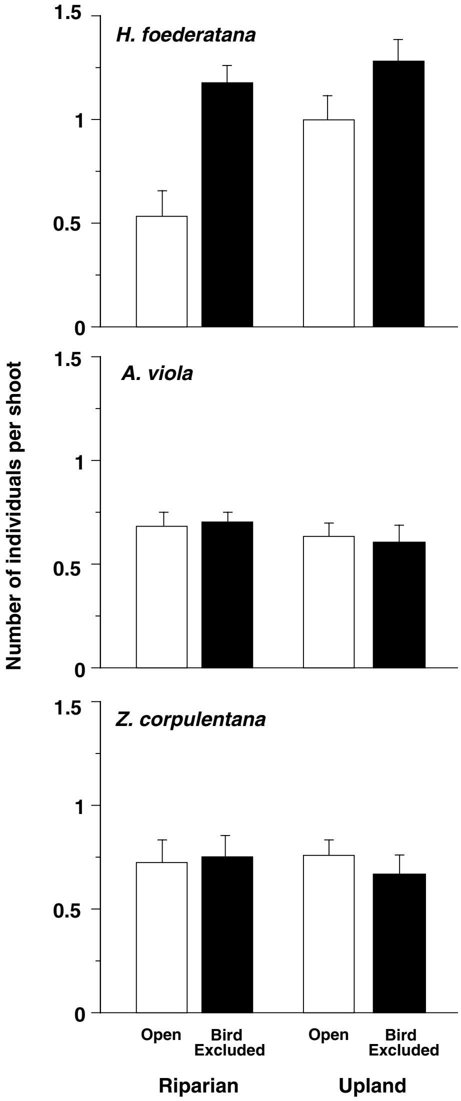

Figure 4 Comparison of leaf roll numbers on bird-excluded and open non-excluded Japanese lilac trees, and between trees in riparian and upland forests, for each of the three predominant Lepidoptera leaf roller species. Vertical bars indicate standard errors.

the differences in foraging site selection between riparian and upland forests (Murakami & Nakano 2001; see also Holmes & Recher 1986). Great tits were frequently found on the forest floor foraging on emerged aquatic insects during the study period (see Murakami & Nakano 2001). Crowned willow warblers frequently foraged by sallying on to flying aquatic insects, whereas marsh tits utilized tree buds in the canopy as their foraging substrate. The analysis of malaise trapping results showed the abundance of aquatic preys to be much higher in the riparian forest, but the abundance of terrestrial insects did not differ between the plots in the two forest types. The distribution pattern of emerged aquatic invertebrates is known to be vertical to the canopy or horizontal on the ground (Power & Rainey 2000). In this study area, swarming by Trichoptera and Chironomids was frequently observed along the stream, whereas emerged Plecoptera and Diptera were frequently observed on the stream bank (M. Murakami, personal observation). Great tits and crowned willow warblers visited and foraged on these resources.

The activity levels of great tits and crowned willow warblers, respectively, were about seven and five times higher in the riparian plots compared with upland ones (Fig. 1). Although the birds in the riparian forest derived much of their energy from aquatic insects, about two-thirds of the diet of the former comprized terrestrial prey, in particular Lepidoptera leaf rollers (Fig. 2). The greater bird population and therefore greater visitation frequency resulted in greater predation pressure on leaf rollers in the riparian forest. Accordingly, the birds thus subsidized can depress the population of *H. foederatana* to greater effect in the riparian forest than in the upland forest, a demonstration of the indirect effect of an aquatic prey input on a terrestrial herbivore through bird predation. The other leaf roller species, *A. viola* and *Z. corpulentana,* however, were not affected by bird predations. Murakami (1999) suggested that conspicuousness of the leaf rolls may be the reason for the differing levels of bird predation on each leaf roller species. *H. foederatana* alters the leaf form to the greatest extent, making it more easy for birds to detect the leaf rolls on the lilac trees.

A recent theoretical consideration has shown that the outcome of a subsidy to a recipient system can vary according to the properties of the predators (Abrams & Matsuda 1996; Huxel & McCann 1998). Polis & Hurd (1996) have shown that orb web spiders subsidized by detritivores from marine guano increased the mortality rate of terrestrial herbivores. The present study also showed that aquatic insect emergence negatively affects leaf rolling Lepidoptera larvae through forest birds. Although bird effects on emerged aquatic insects were not measured in this study, Jackson & Fisher (1986) estimated that only 3% of the biomass of emerged aquatic insects returned to the stream, which suggests a strong impact of birds on the aquatic insect population. This suggests an analogous situation of 'apparent competition' between prey species sharing a common predator (see Holt 1977; Holt & Kotler 1987). Nakano *et al.* (1999b) showed that fish feeding concentrated on accidental fallen inputs of terrestrial arthropods, with no prominent effects on *in situ* prey (aquatic arthropods), when natural terrestrial prey input occurred. In this case, the switching of predation by fishes from aquatic prey to terrestrial insects resulted in a positive effect of the subsidized predators on the *in situ* prey community. The allochthonous resource inputs can lessen the trophic cascade in a recipient community in so far as subsidized predators may shift their foraging activity from *in situ* prey to the allochthonous prey. These revealed that the numerical response or aggregation of predators caused by allochthonous prey inputs can both positively and negatively affect *in situ* prey populations (see also Polis & Hurd 1996; Nakano *et al.* 1999b; Sabo & Power, in press).

In the present study, subsidizing effects of aquatic insect emergence were observed only in the riparian plots, the distribution of insectivorous birds therefore leaning towards the stream and resulting in a heterogeneous pattern of *H. foederatana* mortality within the overall forest. In a recent review, Ostfeld & Keesing (2000) suggested that spatio-temporally pulsed resource inputs induce drastic effects on the dynamics of recipient communities. The present study also suggested that the impact of allochthonous prey inputs can spread throughout a community through a complex network of food webs in a heterogeneous landscape. Future research requires further examination of the complex food web network and the importance of allochthonous prey input on the dynamics and structure of communities in heterogeneous landscapes.

ACKNOWLEDGEMENTS

We thank H. Asano, K. Ono and D. Kishi, and other staff and students of Tomakomai Research Station, for logistical support. M. Power, Y. Ayal and two anonymous referees greatly improved the manuscript. Financial support was provided by the Japanese Ministry of Education, Science, Sport and Culture (Nos. 09NP1501, 11440224). This paper is in memory of the inspiration of T. Abe, M. Higashi, G. Polis and M. Rose.

REFERENCES

Abrams, P. & Matsuda, H. (1996). Positive indirect effects between prey species that share predators. *Ecology*, 77, 610–616.

Holmes, R.T. & Recher, H.F. (1986). Search tactics of insectivorous birds foraging in an Australian eucalypt forest. *Auk*, 103, 515–530.

Holmes, R.T., Shultzs, J.C. & Nothnagle, P. (1979). Bird predation on forest insects: an exclosure experiment. *Science*, 206, 462–463.

Holt, R.D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoret. Population Biol.*, 12, 197–229.

Holt, R.D. (1996). Food webs in space: an island biographic perspective. In: *Food Webs: Integration of Patterns and Dynamics,* eds Polis, G.A. & Winemiller, K.O. Chapman & Hall, New York, pp. 275–285.

Holt, R.D. & Kotler, B.P. (1987). Short-term apparent competition. *Am. Naturalist*, 130, 412–430.

Huxel, G.R. & McCann, K. (1998). Food web stability: the influence of trophic flows across habitat. *Am. Naturalist*, 152, 460–469.

Jackson, J.K. & Fisher, S.G. (1986). Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. *Ecology*, 67, 629–638.

Murakami, M. (1997). Foraging habitat shift in insectivorous birds due to insect herbivores response to strengthening defense of canopy trees. *Ecol. Res.*, 13, 73–82.

Murakami, M. (1999). Effect of avian predation on survival of leaf-rolling lepidopterous larvae. *Reses Population Ecol.*, 41, 135–138.

Murakami, M. & Nakano, S. (2000). Bird function in a forest canopy food web. *Proc. Royal Soc. London B*, 267, 1597–1601.

Murakami, M. & Nakano, S. (2001). Species-specific foraging behavior of birds in riparian forest. *Ecol. Res.*, 16, S99–S110.

Nakano, S., Fausch, K.D. & Kitano, S. (1999a). Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. *J. Anim. Ecol.*, 68, 1079–1092.

Nakano, S., Miyasaka, H. & Kuhara, N. (1999b). Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology*, 80, 2435–2441.

Nakano, S. & Murakami, M. (2001). Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proc. Natl Acad. Sci. USA*, 98, 166–170.

Ostfeld, R.S. & Keesing, F. (2000). Pulsed resources and community 24 dynamics of consumers in terrestrial ecosystems. *Trends Ecol. Evol.*, 15, 232–237.

Polis, G.A., Anderson, W.B. & Holt, R.D. (1997). Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.*, 28, 289–316.

Polis, G.A., Holt, R.D., Menge, B.A. & Winemiller, K.O. (1996). Time, space, and life history: influences on food webs. In: *Food Webs: Integration of Patterns and Dynamics,* eds Polis, G.A. & Winemiller, K.O. Chapman & Hall, New York, pp. 435–460.

Polis, G.A. & Hurd, S.D. (1996). Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *Am. Naturalist*, 147, 396–423.

Power, M.E. & Rainey, W.E. (2000). Food webs and resource sheds: towards spatially delimiting trophic interactions. In: *The Ecological Consequences of Environmental Heterogeneity,* eds Hutchings, M.J., John, E.A. & Stewart, A.J.A. Blackwell Science, Oxford, pp. 291–314.

Sabo, J.L. & Power M.E. (in press). River–Watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology*.

Sokal, R.R. & Rohlf, F.J. (1995). *Biometry*, 3rd edn. Freemann, New York.

Sumner, W.T. & Fisher, S.G. (1979). Periphyton production in Fort River, Massachusetts. *Freshwater Biol.*, 9, 205–212.

Townes, H. (1972). A light-weight malaise trap. *Entomol. News*, 83, 239–247.

Editor, L. Blaustein
Manuscript received 18 October 2001
First decision made 21 November 2001
Manuscript accepted 4 January 2002