Stream meanders increase insectivorous bird abundance in riparian deciduous forests

Tomoya Iwata, Shigeru Nakano and Masashi Murakami

Adult aquatic insects emerging from streams are a fundamental resource sustaining riparian bird communities in broad-leaved deciduous forests. We investigated how stream geomorphology affects the aquatic insect flux and insectivorous bird abundance in 26 riparian-forest plots during spring season in northern Japan. Lateral dispersal of emergent aquatic insects into the riparian forest exponentially decreased with distance from the stream. Similar to aquatic insect distribution, flycatchers and gleaners concentrated their foraging attacks around the stream channel, preying intensively upon emergent aquatic insects. In contrast, bark probers consumed fewer emergent aquatic insects. The abundance of flycatchers and gleaners was closely related to stream geomorphology, whereas that of bark probers was associated with snag density in the study plots. A path analysis showed that the study plots with longer stream channels had greater aquatic insect abundance. This can be interpreted as a consequence of the increased amount of both stream edge and stream surface, where emergent aquatic insects readily penetrate. The increased flux of aquatic insects by stream meanders elevated gleaner abundance in the study plots. In addition, their abundance was directly affected by stream length per se. On the other hand, flycatcher abundance was only directly affected by stream length. Flycatchers, which mainly consumed emergent aquatic insects in the air, may have increased in response to the increase in suitable foraging sites (i.e., open spaces adjacent to perches) accompanying longer stream channels. Although the causal links affecting bird abundance differed among guilds, meandering streams apparently support abundant insectivorous birds in riparian forests. Therefore, to conserve riparian bird communities, it will be necessary to maintain the functions of stream geomorphology that affect the magnitude of energy transfer across the forest-stream interface.

T. Iwata (iwata@js.yamanashi.ac.jp) and S. Nakano, Center for Ecological Research, Kyoto Univ., Hirano-cho, Kamitanakami, Otsu, Shiga 520-2113, Japan (present address of TI: Dept of Ecosocial System Engineering, Yamanashi Univ., 4-3-11 Takeda, Kofu, Yamanashi, 400-8511, Japan). – M. Murakami, Tomakomai Research Station, Hokkaido Univ. Forests, Takaoka, Tomakomai, Hokkaido 053-0035, Japan

An intermixture of heterogeneous habitats has long been considered to have strong impacts on the community structure and dynamics in ecological landscapes (Turner 1989, Forman 1995). One of the major ecological processes in such complex mosaics is the interaction between spatial elements, that is, the flow of energy, materials and organisms among distinct habitats (Turner 1989, Forman 1995). Conceptual and theoretical studies have argued that the physical layout and relative amount of a habitat contained within the landscape can control the cross-habitat transfers of trophic components, the effects often spreading to surrounding communities (Wiens et al. 1985, Stamps et al. 1987, Dunning et al. 1992).

In natural systems, several studies have identified habitat geometry as the best predictor of trophic flow rate, such as movements of dissolved organic carbon (Gergel et al. 1999), detritus (Gasith and Hasler 1976), plants (Hardt and Forman 1989) or animals (Bach 1984) across habitat boundaries (see review by Polis et

al. 1997). The strongest evidence has come from a study on a landscape composed of ocean and island systems. Polis and Hurd (1996) revealed that island size and perimeter largely controlled the rate of detritus input from a productive ocean onto arid islands, with much greater inputs occurring on islands with higher perimeter-area ratios. In addition, such an energy flux subsidizes arthropod detritivores and influences higher trophic levels (e.g., spiders) via island food webs. Thus, island geometry is a major determinant of the biomass and composition of the island animal communities (Polis and Hurd 1996). However, despite the juxtaposition of different habitats, the effects of such habitat geometry on trophic linkages between contiguous habitats are still poorly understood in other landscape types.

Riparian forests, which can be regarded as a zone of contact between terrestrial and stream ecosystems, often support more diverse and abundant communities of invertebrate and vertebrate consumers than do the surrounding uplands (Stauffer and Best 1980, Knopf and Samson 1994, Lachavanne and Juge 1997). There is a growing recognition that energy transport from stream via biological vector, such as aquatic insect emergence, is an important factor maintaining the community diversity and production in the neighboring riparian forest (Jackson and Fisher 1986, Power and Rainey 2000, Nakano and Murakami 2001). Jackson and Fisher (1986) suggested that because only 3% of the biomass of emergent aquatic insects returned to the stream, most of them were preyed upon by a variety of terrestrial insectivores, such as birds, bats, spiders and lizards (see also Gray 1993, Power and Rainey 2000, Gende and Willson 2001, Henschel et al. 2001). The flux of aquatic insects has profound effects upon the maintenance of forest bird communities, especially in highly seasonal environments (Keast 1990, Nakano and Murakami 2001). Nakano and Murakami (2001) found that forest birds in a temperate broad-leaved deciduous forest, in which terrestrial arthropod prey was available only for 4–5 months (during the leafing period) of the year, were strongly dependent upon emergent aquatic insects during the leafless period. They estimated that the contribution of aquatic prey reached 25.6% of the annual total energy budget of the riparian bird community. Moreover, because prey availability in the pre-breeding season, in which females must accumulate reserves for eggs, is responsible for the breeding success of most insectivorous birds (Keast 1990, Tye 1992), aquatic prey supply during spring under a shortage of terrestrial prey biomass could be critical. Therefore, if habitat geometry within a forest-stream landscape (e.g., stream geomorphology) alters the magnitude of aquatic prey flux into a forest, it may also affect the structure and dynamics of the forest bird community.

In this study, we examined how stream geomorphology affected bird abundance in temperate riparian deciduous forests. We hypothesized that landscapes including more highly meandering or larger streams have a greater supply of emergent aquatic insects per unit area of forest and therefore sustain greater bird abundance during spring, when terrestrial prey abundance is low.

Methods

Study site

The study was conducted in riparian deciduous forests of eight streams, discharging into the Pacific Ocean through Tomakomai city (42°38′N, 141°36′E), southwestern Hokkaido, Japan (Fig. 1). The study area is included in the temperate region, with a mean annual temperature of ca 7°C. Apart from a difference in size, the physical attributes of the study streams were similar. Their drainage basins are underlaid by pyroclastic flow and fall deposits and characterized by high soil permeability (Sakuma 1987). Stream discharges of the study streams are relatively stable, with major flood disturbances occurring rarely throughout the year (see Shibata et al. 2001). This hydraulic characteristic suggests that the contribution of deeper ground waters to discharges is larger than that of subsurface flows (Shibata et al. 2001). These low gradient (≤ 1%), cold-spring-fed streams are highly sinuous and have no fringing floodplains, instead having well-developed forests along the edges of the active stream channels. The forest type was homogeneous across the drainage basins, mainly comprising second-growth deciduous forest that had developed after an eruption of Mt Tarumae in 1739.

Bird and insect sampling were made from 10 May to 10 June 2000 in 26 study plots (100 m long × 50 m wide, 0.5 ha area), established along headwater reaches (first- or second-order, 15–80 m in altitude) of the eight streams (Fig. 1 and Table 1). The study plots included a variety of stream geomorphological types, in terms of channel sinuosity (stream length within a plot, range = 108–221 m) and width (mean wetted width within a plot, range = 2.2–7.7 m) (Table 1). The two end points of the centerline (100 m long axis) of each study plot were set on the stream channel. The stream channel between the points was all included within the study plot. The study plots were separated by at least 200 m, being located > 100 m distant from the forest boundaries, which was herein defined as any treeless belts of ≥ 5 m width (excepting streams). Sampling was initiated after confirmation of the arrival of most summer migrants (in early May) and completed before the riparian trees had fully developed their leaves (from mid to late June). The

Fig. 1. Map of the study area with locations of the study plots (open circles) in Tomakomai City, southwestern Hokkaido, Japan. Figures associated with study plots correspond to those listed in Table 1. UN, Uenae Stream; YF, Yufutsu Stream; YB, Yuburi Stream; KS, Kumanosawa Stream; HN, Horonai Stream; US, Usunosawa Stream; KT, Koitoi Stream; NT, Nishitappu Stream.
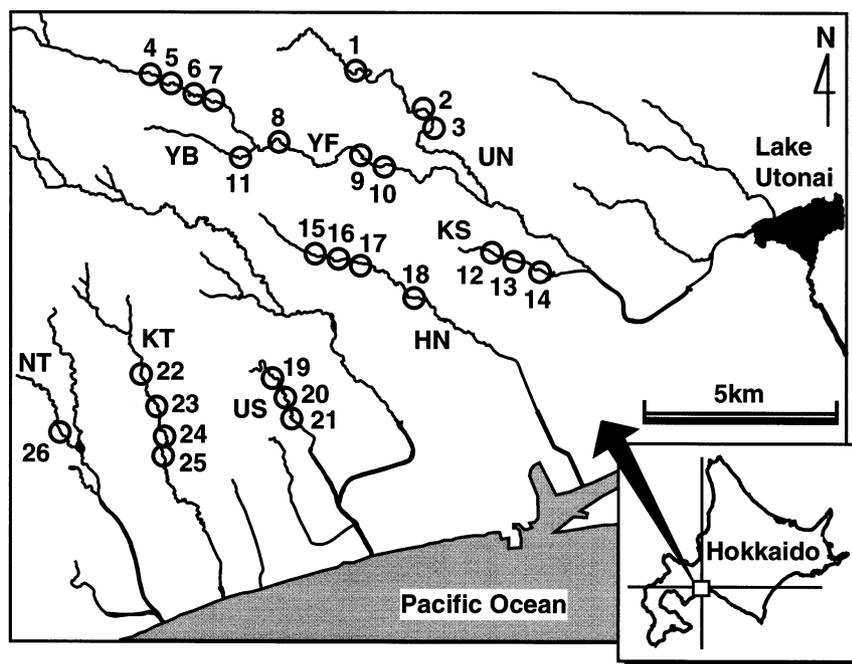
forests in the study plots were dominated by oak *Quercus crispula*, cherry *Prunus sargentii*, Japanese maple *Acer palmatum* var. *matsumurae*, painted maple *Acer mono*, linden *Tilia japonica* and ash *Fraxinus mandshurica*. In the study plots, most canopy tree species broke bud during the period from 25 to 29 May and shed their leaves in mid-October.

Stream geomorphology and riparian forest measurements

The planform geometry of the study reach in each plot was measured with a compass and measuring tape before the sampling period, and drawn to a scale of 1:500. The stream planform was digitized using a scan-

Table 1. A general description of the study reaches in 26 plots.

Number	Elevation (m)	Discharge ($m^3 s^{-1}$)†	Gradient (%)	Stream length (m $plot^{-1}$)	Mean wetted width (m)	Mean depth (cm)
1	40	0.41	0.2	114	3.6	16
2	25	0.54	0.2	153	5.4	26
3	20	0.56	0.2	110	5.3	24
4	80	0.85	1.0	214	5.2	21
5	80	0.91	0.7	125	5.0	26
6	70	0.85	0.7	196	5.1	27
7	65	0.97	0.7	132	6.0	23
8	40	1.28	0.5	133	7.7	25
9	25	1.02	0.4	117	5.4	25
10	25	1.17	0.3	141	5.3	29
11	50	0.28	0.7	165	3.0	17
12	15	0.01	0.3	108	2.7	10
13	15	0.02	0.3	145	2.6	12
14	15	0.04	0.3	154	2.8	16
15	45	0.09	0.3	122	2.6	12
16	45	0.11	0.3	191	2.9	17
17	40	0.12	0.3	207	3.0	14
18	25	0.22	0.3	131	3.4	17
19	25	0.14	0.3	126	2.2	15
20	25	0.12	0.3	145	2.8	16
21	20	0.15	0.3	221	2.4	17
22	45	0.69	0.4	174	5.4	20
23	30	0.73	0.4	152	5.0	20
24	25	0.70	0.4	132	5.0	23
25	25	0.59	0.4	149	5.1	23
26	45	0.32	1.0	149	3.0	18

† Discharge was measured in a base-flow condition during the study.

ner, and the area, length (along the channel axis, hereafter stream length) and mean wetted width (stream width) of the study reach within each plot were determined using NIH Image version 1.6 (National Institutes of Health, Bethesda, USA), a public domain program for image processing and analysis. Channel sinuosity has commonly been expressed by a sinuosity index, which is the ratio of channel length between two points on the channel (the true length of the stream channel) to the straight-line distance between these same points (Allan 1995). Thus it is worth noting that stream length (we obtained) can be converted into the sinuosity index by dividing by 100 m (the straight-line distance between the two end points of the plot). Each study reach was divided into channel-units, classified as glide or pool, according to Bisson et al. (1982). The length and width of each channel-unit was measured so as to obtain the area. The percentage of each of the pools and glides to the reach area was then calculated for each study plot.

The riparian forest condition in each study plot was surveyed using a transect method. Four equally-spaced transects of 4 m width, set perpendicular to stream flow, were established from the stream edge to the margin of each study plot. The transects were established alternately on the left- and right-hand banks of the stream channel. The diameter at breast height (dbh) of all living trees ≥ 3 cm and snags (standing dead trees) ≥ 10 cm in dbh in each transect was measured to the nearest 1 cm. The density (trees m^{-2}) and mean dbh (cm) were then calculated separately for live trees and snags from the data obtained from the four transects in each study plot. The leaf flush of deciduous trees showed drastic changes in vertical foliage structure during the sampling period, preventing the measurement of the seasonal stratified-profile of the vegetation cover. For that reason, we treated the density and mean dbh of both live trees and snags in each study plot as indicators of the riparian forest structure.

Insect sampling and analyses

The distributional patterns of emergent aquatic insects and terrestrial aerial insects in the riparian forest as a function of stream proximity were surveyed by Malaise-trap sampling (Townes 1972). During the sampling period, half-sized Malaise traps (1 m high, 1 m long, 0.6 m wide, made of 0.5 mm mesh) were deployed concurrently in two study plots of the Uenae and Horonai streams, both having relatively straight channels but differing in wetted widths (5.5 m for Uenae and 2.9 m for Horonai). In each plot, the traps were placed along a transect at distances of 0 (over stream), 1, 2, 5, 10, 15, 30, and 60 m at a right angle to the active stream channel (30 cm above the stream surface or ground), and operated for two six day sessions within the sampling period (10–16 May and 16–22 May). The insects

in the Malaise-trap samples were preserved in 70% ethanol, and sorted into aquatic and terrestrial aerial insects in the laboratory, the former being identified to family and the latter to order. The damp mass of each taxon was weighed to the nearest 0.01 mg after blotting for 10 s, and converted into dry mass by multiplying by the taxon-specific damp mass-dry mass ratio (Nakano unpubl.). The abundance of emergent aquatic insects and terrestrial aerial insects at each established point from the stream was then expressed as dry mass per trap per day (mg $trap^{-1}$ d^{-1}).

The Malaise-trap sampling was also conducted in order to estimate food availability for the insectivorous birds in each study plot. Eight 25-m square grids were established in each study plot with red ribbons attached to the tree trunks. In each study plot, a Malaise trap was placed for four or five days 30 cm above the ground or stream surface at the center of a single grid, which was chosen from the eight grids by using random numbers. Such a procedure was repeated six times during the study, avoiding use of the same grid during different sampling periods. Insect biomass in Malaise trap placed close to the ground is known to be a useful indicator of food availability for forest insectivorous birds (Johnson and Sherry 2001). Trapped insects were examined in the same manner as above. The mean of dry mass per trap per day (mg $trap^{-1}$ d^{-1}, n = 6) was used to express the abundance of both emergent aquatic insects and terrestrial aerial insects in each plot.

In addition, the emergence of aquatic insects from the study reach was estimated in each study plot. Three channel-units were randomly chosen from each of the pools and glides. In each individual channel-unit chosen, emerging aquatic insects were collected with a square-pyramid emergence trap (1×1 m area, 1 m high, made of 0.5 mm mesh) set at 1 cm height above the stream surface. The trap was deployed for four or five days and subsequently moved to another selected channel-unit, producing a total of six samples per plot during the sampling period. The samples were preserved in 70% ethanol, identified to family, weighed to the nearest 0.01 mg as damp mass, and converted into dry mass in the same manner as for the Malaise-trap samples. The emergence of aquatic insects was then expressed as dry mass per unit area per day (mg m^{-2} d^{-1}), and was averaged separately for pools and glides (n = 3 for each). Because pools are commonly formed at meander bends in low-gradient streams (Bisson and Montgomery 1996), more highly sinuous reaches may have the greater pool abundance. This in turn may affect the abundance of immature aquatic insects and their emergence from the reach. To evaluate this possible effect of stream geomorphology on the emergence rate, the mean emergence of each channel-unit type (pools and glides) was multiplied by the areal proportion of each channel-unit type and summed for each study reach, so as to obtain an estimate of the reach-

based, habitat-weighted biomass of emerging aquatic insects ($mg\ m^{-2}\ d^{-1}$; hereafter local emergence). Terrestrial arthropods also caught in the emergence traps, which contributed only a minor proportion ($< 5\%$) of the total biomass, were excluded from the analyses.

Bird observation

Bird abundance in each study plot was surveyed on every day not affected by rain, fog or strong wind during the sampling period. All study plots were visited at intervals of five or six days, and censused twice in each of the early morning (05:00–08:00 h), late morning (08:00–11:00 h) and late afternoon (14:30–17:30 h) periods, producing a total of six observations per plot during the sampling period. An observer walked over the entire area of each study plot, following the grid on a systematic basis, all birds seen or heard within the plot being recorded during a 1-h observation period. We attempted to record each individual only once during each observation. Birds that flew over a plot without landing were not included in the data for that plot.

Foraging behavior was also recorded during each observation. When a single foraging bird was encountered, prey attacks (within a 3-min period) were recorded unless other birds were detected. For each prey attack, the distance from the stream, foraging method (sally, glean, peck, or probe), foraging substrate (air, leaves, buds, branches, trunks or ground) and prey item (if seen; identified to the lowest recognizable taxon) were recorded. Identification of prey items (especially tiny arthropods), however, was often difficult. Therefore, after observing the foraging behavior of each individual bird, the observer carefully checked the foraging substrate for any remaining prey or swarm (whenever possible) in the area in which the bird had concentrated its attacks. In the analyses of these foraging records, we used only the first sighting of prey attacks of an individual so as to better satisfy the independence between the records.

A total of 42 species of forest birds was observed during the study, comprising 17 species of year-round residents and 25 species of summer breeding migrants. Of those, 31 species were regarded as insectivorous and were examined in the study (Appendix 1). By reference to Kiyosu (1978) and Takano (1981), all insectivorous birds observed were classified into three foraging guilds, flycatchers, gleaners or bark probers, based on the morphological features that reflect their specific feeding habits (Appendix 1). Birds of the subfamily Muscicapinae, which have a broad and flattened bill and short legs, were assigned to flycatchers. They usually sally out from a perch, capture an arthropod (usually flying insects) and return to the perch. Woodpeckers (Picidae) and nuthatch (Sittidae), which have a stout, chisel-like

bill and stout feet with large toes, and treecreepers (Certhiidae), which have a slender and decurved bill and long curved claws, were classified as bark probers. They usually peck or probe the bark. The other species of Passeriformes observed and oriental cuckoo (Cuculidae) were regarded as gleaners. Gleaners often search leaves, buds, branches or ground for prey (usually stationary arthropods), gleaning them from those substrates, although their feeding habits become occasionally flexible depending on the kind of food available. The abundance of each guild in the study plot (birds $plot^{-1}$) was determined by averaging the number of individuals detected over the six observations.

Data analyses

The abundance of aquatic and terrestrial aerial insects, collected at different distances from the stream channel, was analyzed to test the null hypothesis that such did not vary with distance from the stream. An exponential function, $y = ae^{bx}$, where y is the abundance at distance x, b is the slope of the line, a is the y-intercept and e is the base of natural logarithms, was initially fitted as a model of the distribution of aquatic and terrestrial aerial insects (Petersen et al. 1999, Power and Rainey 2000). The model was fitted in its logarithmic form, $\ln (y) = \ln (a) + bx$, by simple linear regression analysis (y = dry mass [$mg\ trap^{-1}\ d^{-1}$] + 1). When no significant model was obtained from the exponentially-fitted analysis, a linear function, $y = a + bx$, was subsequently fitted to the data after natural logarithmic transformation of both insect abundance and distance. Prior to these analyses, a two-way repeated-measures ANOVA was used to test for the effects of places (Uenae vs Horonai streams) and sampling periods (10–16 May vs 16–22 May) on the abundance of aquatic and terrestrial aerial insects. The analysis revealed that no significant difference existed in aquatic insect abundance between places ($F = 2.18$, $DF = 1$, $p = 0.162$) and between sampling periods ($F = 0.04$, $DF = 1$, $p = 0.845$), as well as no significant interaction effect ($F = 0.32$, $DF = 1$, $p = 0.584$). Similarly, no significant effects of place ($F = 0.62$, $DF = 1$, $p = 0.446$), sampling period ($F = 1.74$, $DF = 1$, $p = 0.208$) and interaction ($F = 1.77$, $DF = 1$, $p = 0.204$) were detected for terrestrial aerial insect abundance. For the exponential and linear fitting analyses, therefore, we combined data from different places and different sampling periods ($n = 32$ in total).

The foraging spaces used by birds were examined in terms of distance from the stream channel. Each of the study plots was divided into six parts, 0 (active stream channel), 0–5, 5–10, 10–15, 15–30 and ≥ 30 m from the stream, and the areal proportion of each part within each plot averaged for all the study plots ($n = 26$). We regarded the mean areal proportion as the availability of each part for bird foraging space. In addition, the

frequency of prey attacks by birds observed in each part was determined by pooling the foraging data from all the study plots (number of prey attacks observed; 94 for flycatchers, 563 for gleaners, and 90 for bark probers). A preference value for each part by the birds was calculated separately for each foraging guild, using the formula of Jacobs (1974):

$$D = (r - p)/(r + p - 2rp)$$

where D is the preference value for a part in the plots, r is the proportion of prey attacks observed in the part, and p is the areal proportion of the part in the plots (availability). The values range from -1 (never used) to $+1$ (only one range used), with negative and positive values indicating avoidance and preference, respectively, and 0 indicating that given part is used in proportion to its availability.

The contributions of aquatic and terrestrial prey to bird diets were estimated for each guild by using data obtained from the foraging observations. We were able to identify or infer prey items on 368 occasions (49.2%; 38 [40.4%] for flycatchers, 272 [48.3%] for gleaners and 58 [64.4%] for bark probers) out of a total of 747 prey attacks observed. The frequency of each prey item was multiplied by the mean individual dry mass of that taxon, which was determined from the samples collected during the sampling period (Iwata unpubl.). The values obtained were summed for order after having been sorted into aquatic and terrestrial prey. The percentage of dry mass contributed by each order was then determined separately for flycatchers, gleaners and bark probers. However, because of the difficulty in differentiating between moth (Lepidoptera) and sawfly (Symphyta) larvae and between spiders (Araneae) and harvestmen (Opiliones) by direct observation, the former were grouped under caterpillars and the latter under arachnids in the analysis. Plant tissues, which accounted for only 6.8% of foraging targets when all of the foraging guilds were combined (0.0% for flycatchers, 9.2% for gleaners, and 0.0% for bark probers), were excluded from the analyses.

Relationships between bird abundance and aquatic and terrestrial variables in the study plots (aquatic: stream length, stream width, local emergence and aquatic insect abundance; terrestrial: live tree density, snag density, mean dbh of live trees, mean dbh of snags and terrestrial aerial insect abundance) were analyzed for each foraging guild using simple linear regression analysis. Because the bird abundance of all guilds (dependent variables) did not agree with the assumption of normality by visual inspections, those were $\ln (x + 1)$ transformed in the analyses (Zar 1984). Furthermore, if the distribution of residuals was not normally distributed, independent variables were $\ln (x)$ or $\ln (x + 1)$ transformed to achieve homoscedasticity and linearity. For guilds significantly related to at least one aquatic

variable in the regression analyses, path analysis was further performed to detect more details pertaining to causality, because complicated causal schemes were likely to exist among the aquatic variables. Path analysis is a useful technique, since it can decompose the overall correlation between two variables into direct effects, indirect effects mediated by other variables, and spurious effects due to common causes (Mitchell 1993). Path coefficients indicate the amount of change in a dependent variable expected from a unit change in an independent variable, with any effect of other independent variables statistically held constant.

We considered that stream length and width affected bird abundance directly as structural characteristics of bird habitat. In addition, the indirect effects of both variables on birds via aquatic insect abundance were likely to exist, because stream geomorphology alters the distribution and flux rate of aquatic insects (Power and Rainey 2000) and thereby may affect bird abundance. The lateral flux of aquatic insects also varies depending on the emergence rate (Power 1995, Power and Rainey 2000). Therefore, local emergence of aquatic insects was also considered as a potential factor affecting birds indirectly via a causal linkage with aquatic insect abundance. We constructed a path diagram connecting these variables to determine which causal relationship most contributed to bird abundance (see Fig. 4). Violations of the homoscedasticity and linearity of the relationships between the variables were countered by $\ln (x)$ or $\ln (x + 1)$ transformation of data (Mitchell 1993). The significance of the path models was tested using a goodness-of-fit test comparing observed and expected correlations of the path diagram (Mitchell 1993). Nonsignificance of the chi-square indicates no significant deviation between the expected and observed correlation matrices under the tested models, indicating that the path model is a valid explanation of the interactions. When the significant effect of exogenous variables (stream length, stream width, or local emergence) on birds was obtained in the path model, robust locally weighted regression (LOWESS: Cleveland 1979) was used to visualize the overall shape of its relationship by using the untransformed data.

In the above analyses, an alpha value of 0.05 was used for statistical significance. Path analyses were performed using Amos ver. 4.0 Student Edition (Small Waters, Chicago, USA). All other analyses were done by Stat-View ver. 5.0 (SAS Inst., Cary, USA).

Results

Spatial distribution of aquatic and terrestrial aerial insects

The abundance of emergent aquatic insects decreased exponentially with distance from the stream (Fig. 2).

Fig. 2. Average abundance of aquatic and terrestrial aerial insects, collected at different distances from the stream channel by Malaise-trap sampling. Means ± SE shown were determined by combining all data collected in two streams (Uenae and Horonai streams) during two sampling periods (10–16 May and 16–22 May) (n = 4 for each point).
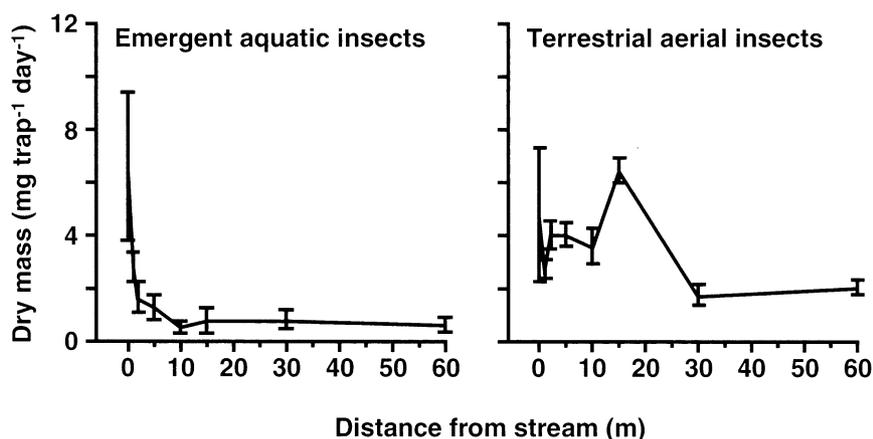
The negative exponential function fitted as a significant model of the dispersal pattern of aquatic insects (Table 2). In particular, the slope was very steep within 5 m of the stream, the abundance at that distance being only 19.6% of that above the stream surface. In contrast, no significant model was obtained from the exponential fitting of terrestrial aerial insect abundance by distance from the stream (Table 2). Even in the linear function model, no significant relationship was obtained between those variables ($R^2 = 0.05$, F = 1.51, p = 0.229, n = 32), indicating that the abundance of terrestrial aerial insects did not vary significantly with distance from the stream.

Bird foraging space and prey items

Flycatchers and gleaners concentrated their prey attacks above streams or at stream edges, foraging considerably on emergent aquatic insects. The preference value (D) indicated that flycatchers strongly selected space above the stream and within 5 m of the stream for foraging, whereas other parts (≥ 5 m from stream) were rarely used (Fig. 3). Although the sample size was small, our foraging observations showed that aquatic prey was the dominant prey item of flycatchers, accounting for 82.3% by dry mass of their diets (Table 3). Gleaners also exhibited a strong preference for the stream edge (0–5 m from stream) as a foraging space, avoiding the parts greater than 5 m distance from stream (Fig. 3). The contribution of aquatic prey to

their diets accounted for 66.7% in dry mass (Table 3). In contrast, bark probers did not exhibit a distinct preference for any part, although their strong avoidance of space above the stream was evident (Fig. 3). Aquatic prey comprised only a small proportion (19.2%) of their diets (Table 3).

Bird abundance in the riparian forest

The abundance of flycatchers and gleaners in the study plots were a significant function of the aquatic variables, while that of bark probers was associated with a terrestrial variable (Table 4). Simple linear regression analyses revealed that the abundance of flycatchers and gleaners were both significantly related with stream length and aquatic insect abundance, indicating that both guilds increased with increasing stream length or aquatic insect abundance in the riparian forest. In contrast to these guilds, bark prober abundance was significantly related only with snag density (a terrestrial variable); the higher the snag density, the greater the abundance of bark probers. Therefore, path analysis was performed for flycatchers and gleaners to evaluate which causal link associated with the aquatic variables most strongly explained their abundance.

The proposed path models significantly fitted the data obtained, and explained 49 and 72% of the variance in abundance of flycatchers and gleaners, respectively (Fig. 4). Non-significant goodness-of-fit tests indicated that no deviations occurred between observed

Table 2. Exponential fitting of dry-mass of emergent aquatic insects and terrestrial aerial insects (dependent variables) in riparian deciduous forests by distance from stream (independent variable).

Dry mass (mg trap^{-1} d^{-1})	ln (a) ± 1 SE	b ± 1 SE	R^2	F	p
Aquatic insects	1.05 ± 0.13	−0.01 ± 0.01	0.19	7.02	0.013
Terrestrial aerial insects	1.44 ± 0.15	−0.01 ± 0.01	0.05	1.53	0.226

Note: simple linear regression analyses (n = 32 for each) were performed using the linearized function [ln (dry mass + 1) = ln (a) + b (distance)] of the exponential model [dry mass + 1 = ae$^{b(distance)}$].

and expected correlation matrices in the models (flycatchers: $\chi^2 = 0.80$, $p = 0.371$; gleaners: $\chi^2 = 0.03$,

Availability n = 26

Flycatchers n = 94
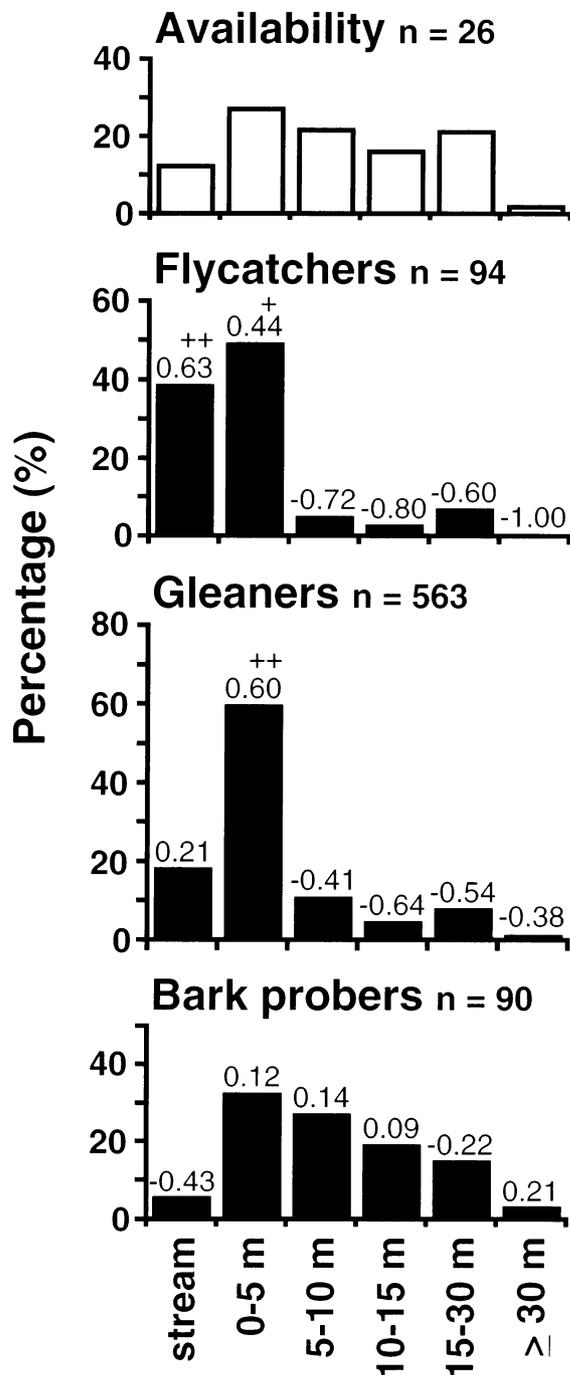
Gleaners n = 563

Bark probers n = 90

Fig. 3. Use of, and preference for, foraging space by birds of each guild in the study plots. Availability of each of six parts (0, 0–5, 5–10, 10–15, 15–30, and ≥ 30 m from active stream channel) is the mean value of the areal proportion of the part in the study plots (n = 26). Jacobs selectivity index (D) is shown at each column. Positive selectivities are denoted by symbols for clarity: (+) values between 0.3 and 0.6; and (+ +) values > 0.6.

$p = 0.869$, DF $= 1$ for each). The abundance of flycatchers was directly influenced by stream length, the path coefficient having a significant positive value (Fig. 4). Although stream length significantly affected aquatic insect abundance in the riparian forests, the direct effect of the latter on flycatchers was not significant (Fig. 4). These results suggest that the significant positive relationship between aquatic insects and flycatcher abundance in the simple linear regression analysis (Table 4) was a spurious effect mediated by multiple positive effects of stream length on both variables (see Fig. 4). Consequently, the indirect effect of stream length on flycatchers via aquatic insect abundance was not significant. Similarly, the abundance of gleaners was directly influenced by stream length (Fig. 4). In addition, gleaner abundance was significantly affected by the indirect causal relationship with stream length via aquatic insect abundance (Fig. 4). For both guilds, stream width and local emergence did not significantly affect bird abundance, path coefficients not differing significantly from zero in any causal links with those variables.

The robust locally weighted regression (LOWESS) described non-linear curves for the relationships between stream length and both flycatchers and gleaners (Fig. 5). Flycatchers steadily increased from 110 to 150 m in stream length, but ceased to do so over greater lengths. Gleaner abundance doubled at about 170 m stream length compared with that at about 110–120 m length and levelled off over greater lengths.

Discussion

Flycatchers and gleaners appeared to spatially track high concentrations of emergent aquatic insects. Most adult aquatic insects stayed close to the stream (particularly within 5 m of the stream), their abundance in the riparian forest declining exponentially with distance from the stream. Similar patterns in lateral dispersal of aquatic insets have been reported previously (e.g., Petersen et al. 1999, Delettre and Morvan 2000, Power and Rainey 2000). Regardless of terrestrial aerial insect distribution, being independent of the stream channel, flycatchers concentrated their foraging attacks on the spaces around the stream channel. Similarly, gleaners strongly selected the stream edge as a foraging space. Although gleaners showed no strong preference for the space above the stream channel, this was probably due to their foraging method in which they searched mainly for stationary prey along the stream banks rather than aerial prey (Iwata unpubl., see Davies 1976, Nakano and Murakami 2001). Both flycatchers and gleaners fed intensively on emergent aquatic insects, comprising 82.3 and 66.7%, respectively, by dry mass of their diets. In addition to aquatic prey, gleaners also consumed arach-

Table 3. Composition of prey items (% in dry mass) in the study plots for birds of each guild. Values were estimated from direct foraging observation data and mean individual dry mass of each prey item. The total number of prey (n) observed for each guild shown in parentheses.

Guild	Aquatic prey					Terrestrial prey								
	EPH	PLE	TRI	DIP	Total	HEM	COL	DIP	LEP-A	CAT	HYM	ARA	OTH	Total
Flycatchers (38)	12.3	26.0	20.0	24.0	82.3	0.0	6.7	1.7	0.0	0.4	0.7	8.2	0.0	17.7
Gleaners (272)	8.7	15.0	17.6	25.4	66.7	0.2	1.0	3.0	1.6	2.3	0.7	23.5	1.0	33.3
Bark probers (58)	0.0	2.5	1.9	14.8	19.2	0.0	34.8	0.0	8.5	0.8	5.3	28.4	3.0	80.8

Abbreviations: EPH, Ephemeroptera; PLE, Plecoptera; TRI, Trichoptera; DIP, Diptera; HEM, Hemiptera; COL, Coleoptera; LEP-A, Lepidoptera (adult); CAT, caterpillar; HYM, Hymenoptera; ARA, Arachnida; OTH, others.

Table 4. Results of simple linear regression analysis using bird abundance as a dependent variable and aquatic or terrestrial variables as an independent variable (n = 26 for all).

Variable	Flycatchers			Gleaners			Bark probers		
	R^2	F	p	R^2	F	p	R^2	F	p
Aquatic									
Stream length (m plot^{-1})	0.42*	17.22	<0.001 (+)	0.53*	26.61	<0.001 (+)	0.02	0.44	0.514
Stream width (m)	<0.01*	0.10	0.754	0.03*	0.81	0.377	0.02*	0.36	0.557
Local emergence (mg m^{-2} d^{-1})	0.10	2.65	0.117	0.05	1.34	0.259	<0.01	0.01	0.909
Insect abundance (mg trap^{-1} d^{-1})	0.32	11.09	0.003 (+)	0.52	25.70	<0.001 (+)	0.06	1.58	0.221
Terrestrial									
Live tree density (trees m^{-2})	0.02*	0.48	0.493	<0.01*	0.05	0.827	0.02*	0.58	0.456
Snag density (trees m^{-2})	<0.01	0.03	0.869	0.09	2.23	0.148	0.22	6.77	0.016 (+)
Mean dbh of live trees (cm)	0.04	0.96	0.336	0.02	0.51	0.482	<0.01	0.19	0.667
Mean dbh of snags (cm)	0.04*	0.95	0.338	0.02*	0.55	0.466	0.10	2.55	0.123
Insect abundance (mg trap^{-1} d^{-1})	0.01	0.24	0.630	0.05	1.25	0.275	<0.01	0.04	0.844

Notes: independent variables with asterisk and all dependent variables were ln (x) or ln (x+1) transformed in the analyses. Plus signs in parentheses indicate positive values of regression coefficient in significant models.
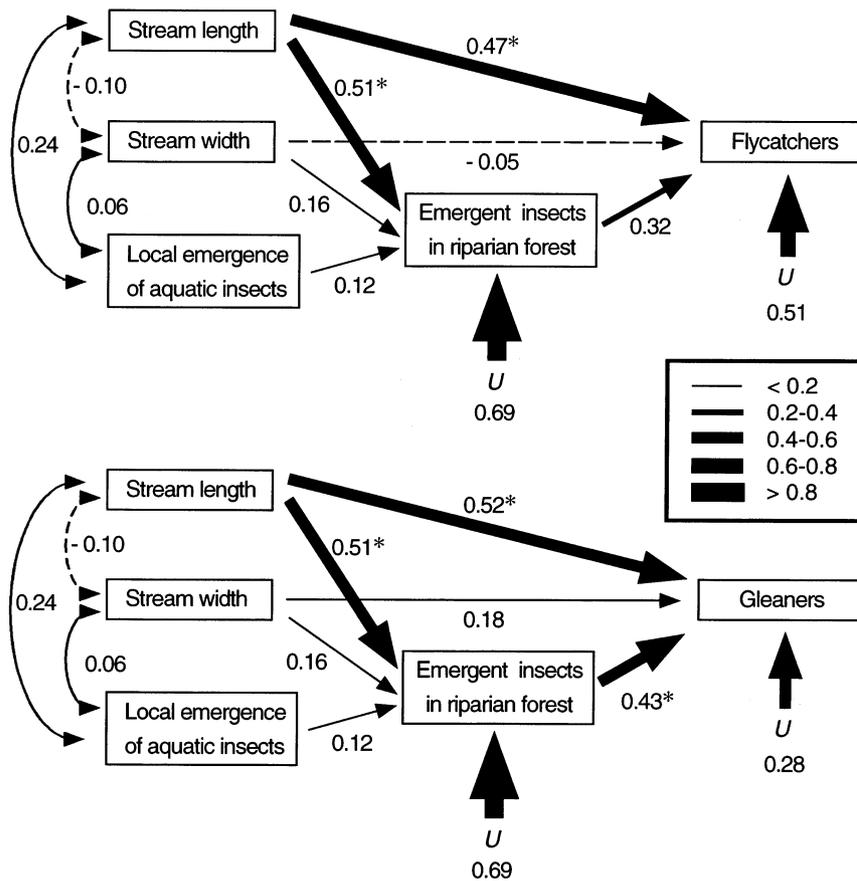
Fig. 4. Results of path analyses for flycatchers and gleaners. Dashed lines denote negative effects; solid lines positive effects. Arrow widths indicate value of path coefficients as presented in the enclosed box (actual values are shown by figures associated with arrows). Values associated with U indicate unexplained variance of dependent variables. Single asterisks indicate that path coefficients are significantly different from zero (p < 0.05). Flycatcher abundance, gleaner abundance, stream length and stream width were ln (x) or ln (x + 1) transformed in the analyses.

nids to a substantial degree (23.5% of diet). Although the Malaise-trap sampling did not quantify the abundance of spiders and harvestmen, our simultaneous study showed that the density of those non-aerial predators along the stream edges was > 2 times higher than that in upland forests 100 m away from the streams and they intensely consumed emergent aquatic insects in the former habitats in this study area (Kato and Iwata unpubl.; see also Jackson and Fisher 1986, Henschel et al. 2001). Thus arachnids possibly mediate the energy transfer from aquatic insects to insectivorous birds (Jackson and Fisher 1986). These results suggested that aquatic insects were an important energy source for flycatchers and gleaners, and their flux affected the spatial distribution of both bird guilds in the riparian forests.

The seasonal contrast between terrestrial and aquatic prey dynamics in the temperate ecosystem is most likely to influence the dependence of flycatchers and gleaners on the flux of aquatic insects. In temperate deciduous forests, terrestrial invertebrate biomass increases with increasing forest productivity (peaking in mid summer) and is depleted during the defoliation period (Keast 1990, Nakano and Murakami 2001). In contrast,

aquatic insect biomass, as well as their flux into the adjacent forest, is greatest in spring after the defoliation period, during which aquatic insect production increases with increases in leaf-litter input and periphyton biomass (Sweeney 1993, Nakano and Murakami 2001). Since the present study was conducted in spring before the riparian forests were leafed out, the high stream production may have driven the energy flow into the adjacent forests, in turn supporting flycatchers and gleaners during a shortage of terrestrial prey biomass (Nakano and Murakami 2001). In contrast, birds categorized as bark probers, such as woodpeckers and nuthatch, preyed mainly upon wood-living insect larvae or pupae (mainly Coleoptera) by pecking or probing. Since the biomass of such prey organisms depends less on the seasonal change in forest production, bark probers do not necessarily rely on aquatic insects, with the result that they avoided treeless stream channels.

The abundance of both flycatchers and gleaners, for which aquatic insects provided significant subsidies, were strongly affected by stream geomorphology, whereas that of bark probers was associated with snag density, a stand characteristic of the riparian forests. The positive relationship between the abundance of

Flycatchers

Gleaners
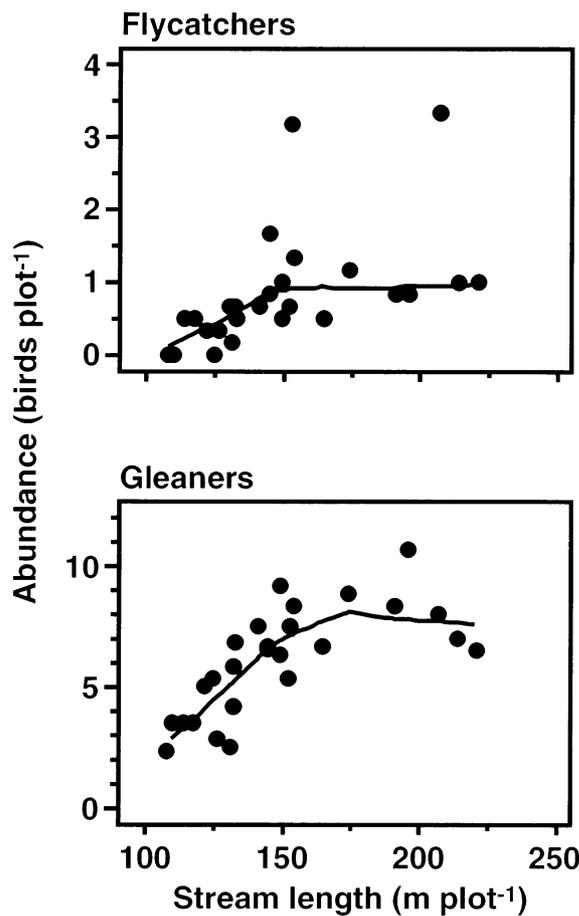
Stream length (m plot⁻¹)

Fig. 5. Relationships between stream length and both flycatchers and gleaners in the study plots. Each data point is for one study plot. Solid lines in data field are LOWESS regression curves.

bark-probing species and snag density has been widely reported (Breininger and Smith 1992, Renken and Wiggers 1993), because snags provide preferred sites for their foraging or cavity nesting (Raphael and White 1984, Olsson et al. 1992). The path analysis indicated that the study plots with longer stream channels (i.e., higher channel sinuosity) had greater aquatic insect abundance. Increases in stream length within a plot can increase the amount of space close to the stream edge, as well as stream area, where emergent aquatic insects readily penetrate. Although stream width and local emergence also had positive (but not significant) effects on aquatic insect abundance, stream length had the more important effect. Thus, the increased density of stream edge, in addition to large area of stream surface, seemed to most strongly increase the flux of aquatic insects into the riparian forests. Such an increased flux of aquatic insects by stream meanders elevated gleaner abundance. In other riparian systems, birds of this type of foraging guild have also been shown as numerically responding to aquatic insect abundance (Davies 1976,

Gray 1993, see also Gende and Willson 2001). In addition, their abundance was directly affected by stream length per se. This is probably because gleaners have increased in response to an increase in the stream edge (their preferred foraging space) accompanying longer stream channels or they have used structural characteristics of stream channels as a clue to identify high availability of aquatic prey, as shown by Orians and Wittenberger (1991). On the other hand, flycatcher abundance was only directly affected by stream length, with the indirect effect of stream length via aquatic insect abundance being not significant. Different from gleaners, the foraging method of flycatchers was restricted, the birds mainly capturing flying insects in the air (83.0% of prey attacks observed). Such a flycatching-technique (i.e., sally) may make it difficult for them to utilize stationary hiding arthropods, necessitating a remarkable dependence on aerial aquatic insects. Because stream meanders increase the space suitable for their foraging on aquatic insects (i.e., more open space adjacent to their perches; see Maurer and Whitmore 1981), it could be more responsible for determining flycatcher abundance than food availability. Our results showed that although the causal links affecting bird abundance differed between flycatchers and gleaners, meandering stream channels apparently increased both insectivores in the riparian forests.

The LOWESS regression curve revealed that both flycatchers and gleaners increased with increasing stream length to some extent, but levelled off in plots greater than ≈ 150 and ≈ 170 m length, respectively. Thus, the straightening of meandering stream channels may be expected to non-linearly influence both guilds. However, the curves had been fitted to untransformed data and expressed overall trends involving multiple causal interrelationships among aquatic- and unexplained-variables. Therefore, details of the mechanisms underlying these patterns need further investigations for clarification. For example, intra- and interspecific competition for limited space (e.g., territoriality) or limited food resource (e.g., aquatic insects) may act to prevent any increase in abundance in forests with longer stream channels (see Petit and Petit 1996, Rodenhouse et al. 1997). These nonlinear responses of bird abundance against stream length seem to have important implications for riverine human activities (e.g., channelization), when designing management plans for the conservation of riparian bird communities.

In conclusion, the present study clearly showed that stream meanders exert powerful influences over adjacent riparian bird communities in a highly seasonal landscape. The high density of stream edge associated with meandering channels can support abundant insectivorous birds by facilitating the energy transfer from stream production. This suggests that the boundary shape, delimited by stream geomorphology, is a spatial feature that strongly affects the degree of trophic con-

nectivity between forest and stream (Wiens et al. 1985, Stamps et al. 1987, Taylor 1993). Hydrological alterations, such as channelization, are now recognized as a major cause of the impoverishment of stream biodiversity (Pringle et al. 2000, Rosenberg et al. 2000). Our results predicted that such river modifications will also influence riparian bird communities. To conserve the communities in a riparian landscape, it will be essential to maintain the interactive energy exchange between forest and stream. This cannot be accomplished without maintaining the functional integrity of the boundary form.

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Appendix 1. Foraging guild and abundance of insectivorous bird species observed in the study plots.

Species	Mean number of birds per plot†
Flycatchers	
Narcissus flycatcher *Ficedula narcissina*	0.35 ± 0.49
Blue-and-white flycatcher *Cyanoptila cyanomelana*	0.29 ± 0.35
Brown flycatcher *Muscicapa latirostris*	0.20 ± 0.28
Gleaners	
Oriental cuckoo *Cuculus saturatus*	0.01 ± 0.03
Gray wagtail *Motacilla cinerea*	0.03 ± 0.13
Olive-backed pipit *Anthus hodgsoni*	0.09 ± 0.14
Brown-eared bulbul *Hypsipetes amaurotis*	0.36 ± 0.33
Bull-headed shrike *Lanius bucephalus*	0.01 ± 0.03
Winter wren *Troglodytes troglodytes*	0.06 ± 0.16
Japanese robin *Erithacus akahige*	0.02 ± 0.07
Siberian blue robin *Erithacus cyane*	0.01 ± 0.05
White's ground thrush *Turdus dauma*	0.01 ± 0.03
Gray thrush *Turdus cardis*	0.18 ± 0.18
Brown thrush *Turdus chrysolaus*	0.04 ± 0.10
Short-tailed bush warbler *Cettia squameiceps*	0.47 ± 0.51
Bush warbler *Cettia diphone*	0.24 ± 0.36
Pale-legged willow warbler *Phylloscopus tenellipes*	0.70 ± 0.54
Crowned willow warbler *Phylloscopus occipitalis*	0.71 ± 0.49
Long-tailed tit *Aegithalos caudatus*	0.22 ± 0.29
Marsh tit *Parus palustris*	0.36 ± 0.42
Coal tit *Parus ater*	0.24 ± 0.50
Varied tit *Parus varius*	0.12 ± 0.23
Great tit *Parus major*	0.74 ± 0.72
Japanese white-eye *Zosterops japonica*	0.02 ± 0.07
Black-faced bunting *Emberiza spodocephala*	2.70 ± 1.28
Eurasian jay *Garrulus glandarius*	0.15 ± 0.14
Bark probers	
Great spotted woodpecker *Dendrocopos major*	0.09 ± 0.14
White-backed woodpecker *Dendrocopos leucotos*	0.01 ± 0.03
Pygmy woodpecker *Dendrocopos kizuki*	0.22 ± 0.30
Nuthatch *Sitta europaea*	0.27 ± 0.34
Tree creeper *Certhia familiaris*	0.15 ± 0.28

† Means ± SD determined by averaging abundance data from all study plots (0.5 ha, n = 26).