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## Do seasonally fluctuating aquatic subsidies influence the distribution pattern of birds between riparian and upland forests?

Received: 11 April 2006 / Accepted: 23 June 2006 / Published online: 27 September 2006  
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**Abstract** Seasonal fluctuation of allochthonous subsidies influences food web structure and dynamics in recipient communities. This study investigated whether aquatic subsidies influence the dynamics of insectivorous birds in entire catchment. We estimated the prey biomass and bird density in riparian and upland habitats in three catchments in temperate deciduous forests in Hokkaido, Japan. Aquatic prey was found only in riparian forests and the biomass peaked in early spring, while terrestrial prey was equally distributed between habitats and increased in biomass in late spring. Bird density was higher in riparian than in upland forests before bud break, when the biomass of aquatic insects peaked, but was similar in both forests during the rest of the seasons. These results suggest that aquatic prey subsidies are used not only by birds inhabiting riparian forests, but also by birds associated with upland forests. Aquatic prey subsidies may be particularly important in the spring as a critical food resource for survival and the breeding activities of birds, thereby, influencing the population dynamics of bird communities.

**Keywords** Allochthonous input · Insectivorous songbirds · Prey switching · Terrestrial productivity · Catchment

### Introduction

The movement of resource subsidies from one habitat to another can strongly influence food web structures and dynamics in adjacent communities (Polis and

Hurd 1995; Huxel et al. 2002; Sabo and Power 2002a, 2002b; Baxter et al. 2005). While some studies assume that these allochthonous subsidies are constant over time (Polis and Hurd 1996), seasonal variability in quality and quantity of subsidy input is frequently observed (Nakano and Murakami 2001). Theoretical models show that seasonally fluctuating subsidies stabilize food web dynamics by raising the minimum carrying capacity of recipient habitats during the period of low in-situ productivity if consumers switch their prey preferences to correspond with prey availability (Post et al. 2000; Takimoto et al. 2002). Such subsidy dynamics have been observed (Polis et al. 1997; Nakano and Murakami 2001), but these investigations were limited in their spatial scope to habitats near boundaries. Because subsidies create a mosaic of resource patches across the landscape (Jackson and Fisher 1986), their effects are expected to be carried farther away from boundaries by highly mobile consumers (Rose and Polis 1998; Power et al. 2004).

The emergence of adult aquatic insects from streams may create temporal and spatial heterogeneity in prey availability for insectivorous predators. For instance, in temperate deciduous forests, insectivorous birds in riparian zones forage extensively for aquatic insects in early spring, when terrestrial resources are limited (Nakano and Murakami 2001). However, as terrestrial productivity exceeds the aquatic system during the summer, many birds switch their foraging to terrestrial invertebrates. Distributions of aquatic insects are generally restricted to riparian forests (Gray 1993; Nakano and Murakami 2001), thereby, creating spatial heterogeneity for resources across the catchment. However, it is not known whether such temporal and spatial resource heterogeneity influences community dynamics of birds across the entire catchment.

If aquatic resources are essential for birds in times of low terrestrial productivity, birds with upland territories are expected to aggregate in riparian forests during the early spring. During the summer, the bird distribution between these habitats should become more similar, as

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terrestrial productivity increases. Furthermore, species may respond differently to aquatic resources because of constraints on foraging behaviors (Murakami and Nakano 2001). Generalist species that are capable of switching their prey items between aquatic and terrestrial invertebrates are expected to shift their foraging habitats more than either aquatic or terrestrial prey specialists.

In this study, we measured the seasonal changes in prey abundance and bird density at riparian and upland forest plots. Bird density was higher in riparian than upland plots when aquatic prey was abundant, but was evenly distributed as terrestrial prey biomass increased. In addition, species differed in the degree of aquatic prey use and habitat shift: prey generalist species shifted their foraging habitats more than specialist species.

## Materials and methods

### Study sites

The study was conducted in temperate deciduous forests in the Tomakomai Experimental Forest (TOEF) and the adjacent National Forest (42°41'N, 141°31'E–141°36'E) in Hokkaido, the northern island of Japan (Fig. 1). The study area encompasses the catchments of Horonai (24 km<sup>2</sup> in drainage area, 12.7 km in total length, 2–5 m in stream width), Kumanosawa (6.8 km<sup>2</sup>, 2.5 km, 1–2 m), and Tomakomai (52 km<sup>2</sup>, 24.6 km, 2–7 m), all of which are spring-fed and rarely disturbed by floods. The forests are fairly homogeneous across the catchments, and are mainly composed of second-growth deciduous trees, dominated by oak (*Quercus crispula*), maple (*Acer palmatum* and *A. mono*), and cherry (*Prunus sargentii*).

Insect sampling and bird censuses were conducted in 24 study plots (100×100 m) established in riparian and upland forests within the three catchments (Fig. 1). We established four riparian plots randomly along the headwater of each stream, and four upland plots approximately 500 m away parallel to each stream. All

study plots were separated by at least 200 m. Vegetation surveys of tree and shrub species were conducted with a 30×2 m transect per plot. There were no significant differences in the total basal area, species richness, or the Shannon's species diversity index of trees/shrubs between riparian and upland habitats and among the three catchments (two-way ANOVA with habitat and stream as factors,  $P > 0.07$  for all comparisons).

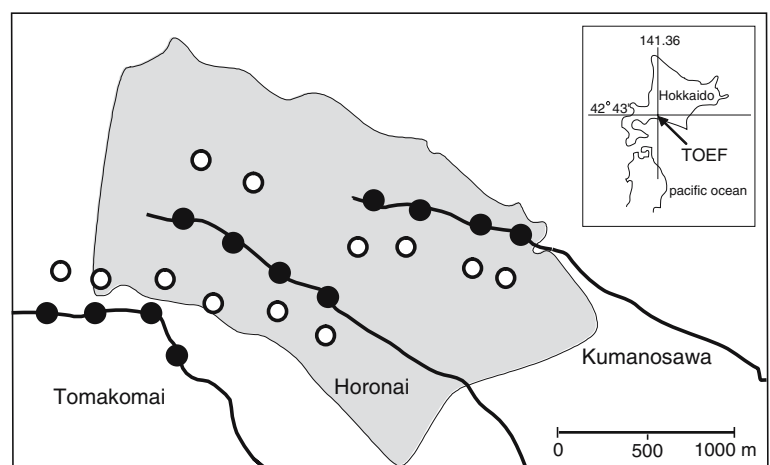
### Study periods

Insect sampling and bird censuses were performed ten times between May 2001 and July 2002: mid-spring (MSP: 5–20 May), late spring (LSP: 21 May–11 June), early summer (ESU: 11 June–2 July), late summer (LSU: 16 July–6 August), and fall (FL: 25 October–8 November) in 2001; winter (WT: 30 January–21 February), early spring (ESP: 18–28 April), mid-spring (5–16 May), late spring (26 May–12 June), and early summer (18 June–3 July) in 2002. The sampling periods were chosen to match the major phenological changes in canopy trees because the tree phenology strongly influences the abundance of terrestrial invertebrates (Nakano and Murakami 2001). The canopy tree broke buds during late spring, but occurred a few days earlier in upland than in riparian plots. The canopy closed completely by the end of early summer and mature leaves persisted throughout late summer until defoliation in October. Fall sampling was conducted after defoliation, but before snowfall. Snow persisted during winter sampling and melted before early-spring sampling.

### Estimation of prey biomass

Invertebrate biomass was surveyed once at each study plot during each sampling period. We collected aquatic and terrestrial flying insects using a half-sized Malaise trap [1 m high×1 m long×0.6 m wide, made of 0.5-mm mesh (Townes 1972)] per plot, deployed for 7 days. The traps were placed directly on the ground next to stream

**Fig. 1** Map of study plots encompassing three catchments in Tomakomai Experimental Forest (TOEF: shaded area) and the adjacent National Forest. The lines indicate the three streams, Tomakomai, Horonai, and Kumanosawa. The closed and open circles show the location of riparian and upland plots, respectively



edges in riparian plots and in the middle of each upland plot. Terrestrial arthropods on tree foliage were collected from three oak trees per plot by tapping branches (> 1.5 m high) with a wooden stick and collected arthropods that dropped onto a sheet (1×1 m in area) spread below (Nakano and Murakami 2001). Leaves were carefully checked for remaining invertebrates. During the winter, prey abundance was surveyed at only eight plots in the Horonai Stream catchment (four in each habitat type), due to difficulties in accessing the other catchments.

All insects collected were preserved in 70% ethanol, identified to order (to family for Diptera and Coleoptera), and sorted into aquatic and terrestrial groups (see Nakano and Murakami 2001 for details). The wet weight of each order or family was measured to the nearest 0.01 mg after blotting for 10 s. Their values were converted to dry weight via taxon-specific wet/dry regressions obtained from previous research (Kawaguchi and Nakano 2001). The biomass is expressed as dry mass (mg) per trap per day for Malaise samples and dry mass (mg) per square meter for foliage samples.

#### Bird observation

Bird surveys were conducted by a single observer (A. Uesugi) between dawn and 1100 hours on days of clear visibility with no strong wind. The observer visited each plot four times in a random order during each sampling period. Each observation period lasted for 25 min, and all birds seen or heard within the plot were recorded. Observation was primarily performed at the mid point of the plot, but birds detected near the edge were approached by the observer to determine whether the individual was inside the study plot or not. We avoided multiple recordings of individuals per observation period by keeping track of the locations in which individuals were initially found. A total of 8,460 observations, including 49 forest bird species, were recorded during the entire study period. Of those observations, 7,147 (84% of total) were of 18 common species (9 summer migrants and 9 year-round residents), which we selected as focal species for analyses (see Appendix).

The foraging behavior of birds in riparian plots was observed to identify prey items in mid-spring, early summer, and fall of 2001 and in winter 2002. This observation was performed between 0700 and 1100 hours only in riparian plots, since aquatic prey was absent in upland plots. When a bird was encountered, we followed it for 1 min or until we lost sight of it and recorded its prey items. Since the identification of prey items was often difficult, especially for swarming aquatic insects, we approached the foraging location to check for remaining prey. This often allowed us to estimate prey identity (see Nakano and Murakami 2001). Prey types were classified as adult aquatic invertebrates, terrestrial invertebrates, or plant materials, such as seeds and pollen. We identified prey categories for 1,445

observations (61.5%) from a total of 2,348 foraging observations made.

#### Data analysis

We analyzed the biomass of arthropods separately for adult aquatic insects, terrestrial flying insects collected in Malaise traps, and for arthropods collected from foliage. Bird density was also analyzed separately for summer migrants and year-round residents. The bird density was estimated by averaging the number of birds observed during the four visits for each season, and expressing density as birds per hour per hectare. The biomass of arthropods and the density of birds were compared between habitats (riparian and upland) and the catchments of three streams (Horonai, Kumanosawa, and Tomakomai), with repeated measures for seasons (sampling periods), using two-way repeated-measures ANOVA with mixed procedure. Differences between habitats for each season were further tested by unpaired t-tests corrected with Bonferroni adjustment. Both invertebrate and bird data were log-transformed for the analysis. Analyses were performed using SAS software, Version 8 (SAS Institute, Inc., Cary, USA).

For each bird species, aquatic prey use ( $P$ ) in riparian forests was calculated as a proportion of aquatic prey attack to the total amount of foraging observed during each season. A value for aquatic prey preference in each bird species was determined using Jacobs' selectivity index (Jacobs 1974):

$$D = \frac{r - p}{r + p - 2rp}$$

where  $D$  is the preference value for adult aquatic insects,  $r$  is the proportion of prey items that were aquatic, and  $p$  is the proportion of aquatic insect biomass in the study plots. The value of Jacobs' selectivity index ranges from  $-1$  to  $+1$ , with negative and positive values indicating the avoidance and preference for adult aquatic insects, respectively.

The relationship between the degree of aquatic prey use ( $P$ ) and habitat shift was examined using a second-degree polynomial regression model. We defined the degree of habitat shift for a particular species ( $H$ ) as the change in proportion of individuals in riparian habitats from mid- to late spring:

$$H = \text{mean} \left[ \frac{R_m}{R_m + U_m} - \frac{R_l}{R_l + U_l} \right]$$

where  $R_m$  and  $U_m$  are the bird abundance in riparian and upland plots in mid-spring, respectively and  $R_l$  and  $U_l$  in late spring, respectively. Positive values of  $H$  indicate that more individuals are found in riparian than in upland plots, and that the difference in abundance between the habitats is greater in mid-spring than in late spring. The values were averaged over 2 years. This analysis was conducted using the statistical package Stat View, Version 5.0.1 (SAS Institute, Inc., Cary, USA).

## Results

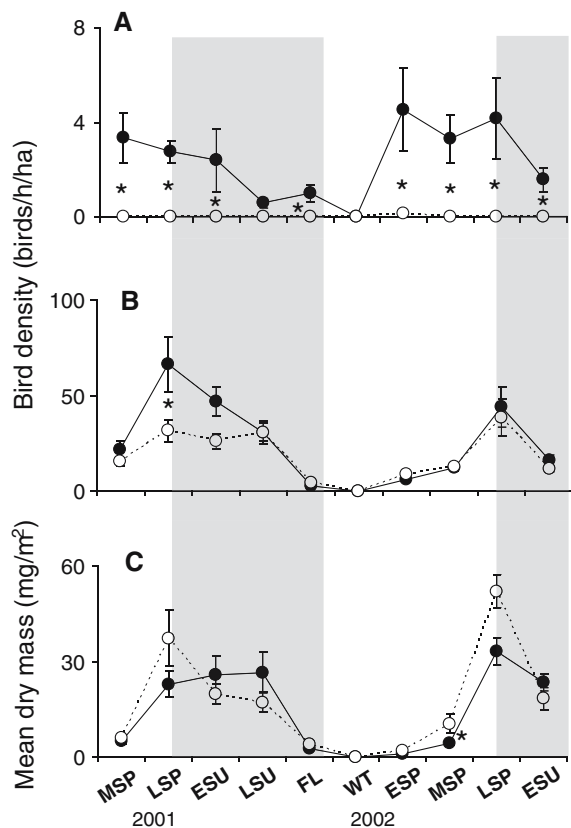
### Insect abundance

Adult aquatic insects were found almost exclusively in the riparian forests, and the biomass peaked in early to mid-spring before bud break (Fig. 2a). There was no effect of catchment ( $F_{2, 18}=0.46$ ,  $P=0.64$ ). Significant habitat $\times$ season interaction ( $F_{9, 162}=5.64$ ,  $P<0.0001$ ) indicated that between-habitat differences in aquatic insect biomass varied across seasons. Nevertheless, abundance was higher in riparian than upland habitats in all seasons (d.f. = 22,  $t>3.4$ ,  $P<0.001$  for all comparisons).

Terrestrial flying insects were found in both riparian and upland habitats with no habitat effect ( $F_{1, 18}=0.99$ ,  $P=0.33$ ). Their biomass was relatively low in early to mid-spring, rapidly increased as trees leafed out in late spring, and dropped to almost zero in fall and winter (Fig. 2b). This general pattern was observed in all three

catchments, although the biomass was exceptionally high in Kumanosawa riparian plots in late spring 2001 (effect of catchment:  $F_{2, 18}=6.65$ ,  $P=0.006$ ). There were season $\times$ habitat interactions ( $F_{9, 162}=3.01$ ,  $P=0.002$ ), but no differences in biomass were observed between riparian and upland habitats in all seasons ( $t<2.7$ ,  $P>0.12$  for all comparisons).

Terrestrial insects on foliage were equally abundant in riparian and upland habitats ( $F_{1, 18}=2.73$ ,  $P=0.11$ ), and showed a seasonal pattern similar to the terrestrial flying insects (Fig. 2c). An increase in late spring was largely due to the emergence of lepidopteran larvae, which accounted for more than 70% of the total biomass. There was no effect of catchment ( $F_{2, 18}=0.34$ ,  $P=0.71$ ) and no differences between riparian and upland habitats in each season ( $t<2.9$ ,  $P>0.07$  for all comparisons). These results indicate that terrestrial invertebrates were evenly distributed between riparian and upland forests during each season.



**Fig. 2a–c** Seasonal changes in the biomass of potential prey arthropods. **a** Adult aquatic insects. **b** Terrestrial flying insects. **c** Arthropods on foliage. Closed circles represent the biomass in riparian three plots and open circles in upland plots. The asterisks indicate significant between-habitat differences (unpaired *t*-tests with Bonferroni adjustment for ten tests). The sampling periods are indicated as follows: MSP mid spring; LSP late spring; ESU early summer; LSU late summer; FL fall; and WT winter (see Study periods section for specific dates). The shaded areas represent periods of leafing in canopy trees. Data shown include means and standard errors

### Bird diet and distribution pattern

Birds observed in riparian habitats preyed upon adult aquatic insects frequently in the spring (39.4% of total observation, Table 1), but rarely in the summer (5.6%). In the spring, seven bird species preferred adult aquatic insects to terrestrial flying insects as prey ( $D>0$ ). During the fall and winter, non-migratory resident birds preyed on adult aquatic insects for 27.4% and 9.0% of the time, respectively (Table 1).

Bird densities for both residents and migrants were, in general, higher in riparian than upland habitat plots in early to mid-spring, but were similar during other seasons (Fig. 3a, b). Similar distribution patterns were observed in all three catchments (no catchment effect:  $F_{2, 18}=2.49$ ,  $P=0.11$  and  $F_{2, 18}=0.85$ ,  $P=0.44$  for migrants and residents, respectively), but the seasonal pattern in bird density was different between habitats (season $\times$ habitat interaction:  $F_{9, 162}=7.62$ ,  $P<0.0001$  and  $F_{9, 162}=2.53$ ,  $P=0.01$  for migrants and residents, respectively). Migrants showed higher abundance in riparian than upland habitat in mid-spring during both years ( $t>5.7$ ,  $P<0.001$ ), and the difference was already prominent in early spring 2002 ( $t=3.3$ ,  $P=0.02$ ). In late spring, the migrant bird density decreased in the riparian habitat, but increased in the upland habitat, eliminating the difference between the two habitats ( $t>2.5$ ,  $P>0.18$ , Fig. 3). Residents showed no difference between habitats in any season ( $t<2.7$ ,  $P>0.15$  after Bonferroni correction).

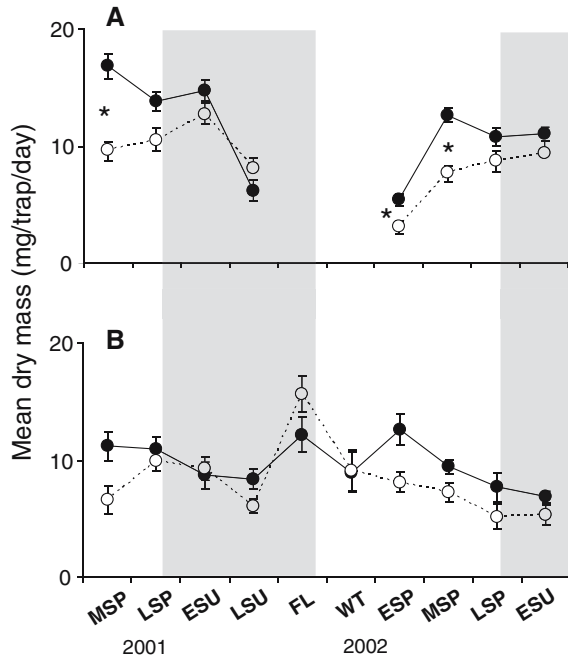
The above seasonal distribution patterns also varied between bird species. Generalist species that used aquatic prey at an intermediate level showed the highest degree of habitat shifts, while specialist species that foraged on aquatic prey at low or high levels were less likely to shift (Fig. 4). This relationship was significant when the data was fitted to the second-degree polynomial regression model ( $P=0.03$ ,  $r^2=0.38$ ), but not when fitted with the linear regression model ( $P=0.13$ ,  $r^2=0.14$ ).

**Table 1** Percentage of aquatic prey items in diets of bird species foraging in riparian forest plots in the spring, summer, fall, and winter. Sample sizes ( $n$ , the number of observations) are shown in parentheses

Species	Spring	Summer	Fall	Winter	
Summer migrants					
BF	Brown flycatcher	84.9 <sup>a</sup> (53)	25.9 (27)	–	–
PWW	Pale-legged willow warbler	80 <sup>a</sup> (40)	29.2 (24)	–	–
CW	Eastern crowned willow warbler	76.9 <sup>a</sup> (26)	5.56 (36)	–	–
BWF	Blue and white flycatcher	70.4 <sup>a</sup> (27)	26.3 (19)	–	–
GTH	Japanese grey thrush	62.5 <sup>a</sup> (16)	0 (16)	–	–
NF	Narcissus flycatcher	52.4 <sup>a</sup> (42)	8.16 (49)	–	–
TP	Olive-backed tree pipit	42.2 (45)	0 (16)	–	–
BFB	Black-faced bunting	40 (40)	0 (51)	–	–
BW	Short-tailed bush warbler	38.5 (26)	0 (16)	–	–
Residents					
GT	Great tit	55.6 <sup>a</sup> (72)	0 (49)	29.4 (17)	0 (2)
NH	Nuthatch	46.4 (28)	0 (33)	8.2 (49)	13.2 (38)
TC	Tree creeper	37.9 (29)	0 (5)	0 (10)	22.2 (18)
PWP	Japanese pigmy woodpecker	20.9 (43)	0 (16)	0 (12)	0 (11)
MT	Marsh tit	13.2 (53)	0 (66)	6.3 (64)	5.1 (39)
VT	Varied tit	7.41 (27)	0 (2)	0 (2)	50.0 (2)
CT	Coal tit	0 (78)	– (0)	– (0)	0 (1)
GWP	Great spotted woodpecker	0 (29)	0 (17)	0 (6)	0 (3)
LT	Long-tailed tit	0 (24)	0 (3)	0 (20)	0 (8)
	All species	39.4 (698)	5.6 (445)	27.4 (180)	9.0 (122)

– Absence of data

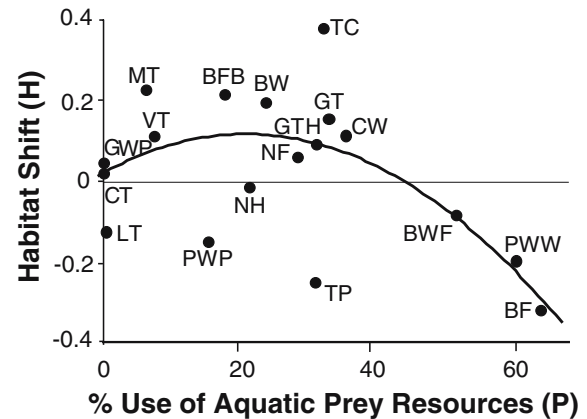
<sup>a</sup>Positive preferences for aquatic prey by Jacob's selectivity index ( $D$ )



**Fig. 3a, b** Seasonal changes in bird density (birds/h/ha) for summer migrants (**a**) and year-round residents (**b**) in the riparian (closed circles) and upland (open circles) habitat plots from mid-June 2001 to early summer 2002. Details are in Fig. 2

## Discussion

The bird distribution patterns were consistent with our hypothesis that birds move between habitats in response to fluctuating resource availability. The presence of aquatic insects was restricted to riparian habitat and became available when terrestrial resources were limited. During the early spring, the total biomass of aquatic insects (Fig. 1a) was lower than terrestrial flying insects



**Fig. 4** Regression plots for the degree of habitat shift ( $H$ ) against the percentage use of aquatic resources ( $P$ ). Each point indicates a particular species (see Appendix for abbreviation codes). The fitted line reflects a second-degree polynomial regression ( $Y = -0.012 + 0.009X - 0.0002X^2$ ;  $P = 0.03$ ,  $r^2 = 0.37$ , see Materials and methods section)

(Fig. 1b), but seven species of birds selectively preyed upon the aquatic insects, indicating that the aquatic insects may be more important as prey resources than terrestrial flying insects. This preference for aquatic insects may be due to their slow movements and higher nutritional quality, as suggested elsewhere (Smith et al. 1998; Nakano and Murakami 2001; Iwata et al. 2003). The late-spring emergence of lepidopteran larvae homogenized the resource environment and reduced the relative importance of aquatic subsidies. At this time, birds that had been foraging on adult aquatic insects in riparian forests switched prey items to terrestrial invertebrates. Seasonal variation in foraging strategy has been reported for various species of birds (Smith et al. 1998; Murakami and Nakano 2001), and the ability to

switch foraging method is thought to maximize energy gain during periods of low resource supply (Keast 1990).

Previous studies have examined the effect of aquatic subsidies on insectivorous birds (Gray 1993; Smith et al. 1998; Gende and Willson 2001; Nakano and Murakami 2001), but these investigations were limited to riparian forests. Our study on bird distribution patterns indicates that the effect of subsidies is carried throughout the catchment. High riparian density in early spring suggests that birds establishing territories in upland habitats may commute to riparian forests, which is consistent with the reports of birds foraging outside nesting territories (Davies 1976; Nagai 2000). In summer, birds dispersed throughout the catchment and were observed foraging with increased proximity to their nests (A. Uesugi, personal observations).

The seasonal distribution pattern was more prominent in migratory birds than non-migrants, suggesting that aquatic insects are an especially important resource to early migrants, as demonstrated by other works (McCarty 1997; Smith et al. 1998). However, not all species responded to the aquatic subsidies in the same manner. Prey generalists that use aquatic prey at an intermediate level exhibit a higher degree of habitat shift than specialists of either aquatic or terrestrial prey (Fig. 4). Generalists' ability to shift foraging habitat suggests that the spatial and temporal variation of aquatic subsidies could maintain high species diversity by allowing generalists, which may be otherwise competitively excluded by specialists, to persist within a catchment.

The seasonal patterns we present are indicative of catchment-wide movements of birds across habitats. However, our methods of inferring bird movements have some limitations. First, while our method allows us to infer the general patterns of seasonal changes over a large spatial scale, it lacks resolution at an individual level because we did not track each individual bird. Individual tracking methods, such as radio telemetry, allow researchers to determine the exact movement of the bird, and have been implemented in behavioral studies in passerines (Goguen and Mathews 2001; Norris and Stutchbury 2002). However, tracking methods are limited by expense, sample size, and the temporal and spatial scales that can be implemented. Our results indicate dynamic bird movements in the spring, but individual bird behaviors can be further examined with radio telemetry to complement this information.

Increased upland bird density during the late spring may not completely reflect the movement of birds from riparian forests. Since the total area of riparian forest (< 100 m from a stream) in the study catchments is approximately 10% of upland forest (see [Study sites](#) section), the individuals that left the riparian may not account for the total increase in bird abundance in the upland plots. Although most migrants arrived before the mid-spring sampling periods (A. Uesugi, personal observations), the influx of late migrants to upland

forest could contribute to this increase. Nevertheless, the bird density in all riparian plots decreased after bud break, indicating that at least some birds foraging near streams moved to upland forests.

Other factors, aside from aquatic subsidies, may also influence the seasonal distribution patterns of birds. Strong territoriality may negatively impact potential habitat shifts for certain species. For example, Narcissus flycatchers display a high degree of prey switching, but do not appear to shift foraging habitat. Since male Narcissus flycatchers defend their established territories constantly by chasing intruders away (A. Uesugi, personal observations), they are probably less likely to forage outside of their territories.

Forest vegetation structure is another factor that may influence bird distribution patterns in catchments (Jackson and Fisher 1986; McGarigal and McComb 1992; Murray and Stauffer 1995; Lock and Naiman 1998). For example, bird abundance is positively correlated with the percentage of deciduous trees in species that require hardwoods for successful breeding (Lock and Naiman 1998). We minimized the effect of vegetation structure by conducting surveys in relatively homogenous forests across the catchment (see [Materials and methods](#) section). Our methods, therefore, allowed us to examine the direct effect of aquatic prey on bird distributions.

The input of aquatic prey may be critical for maintaining bird populations within catchments. Because spring food availability is most limited before bud break, over-wintering passerines often suffer severe mortality (Payne and Wilson 1999), and aquatic prey subsidies may facilitate bird survival during this period. Migrants encounter less phenologically advanced vegetation as they migrate north, and aquatic prey subsidies are known to provide them with food resources critical to their recovery from the long trip (Ewert and Hamas 1995). Subsidies may also enhance the breeding success of birds by supporting territorial and courtship activities, as well as influencing the timing of egg-laying (Svensson and Nilsson 1995) and clutch sizes (Nager et al. 1997; Olsson et al. 2001).

The effects of aquatic subsidies may be more widespread in landscape than has been previously appreciated. Aquatic resources can influence the population dynamics of highly mobile consumers that are associated with habitats beyond the boundary areas, such as coyotes (Rose and Polis 1998), bears (Ben-David et al. 1998), bats (de Jong and Ahlen 1991; Power et al. 2004), and rodents (Stapp and Polis 2003). As a consequence, energy and nutrients from aquatic resource subsidies will be distributed throughout catchments by their movements. Our findings suggest that the effects of seasonally fluctuating subsidies could propagate throughout catchments via the movement of insectivorous birds. As a result, these movements of consumers may strongly affect population dynamics and food web structures.

**Acknowledgments** We thank M. Toda, K. Fausch, C. Baxter, and T. Iwata for their inspiring comments regarding the study. T. Connallon greatly improved the manuscript. We are also grateful to the many staff and graduate students at Tomakomai Research Station, Hokkaido University, Japan, for their support during the

study, especially to T. Ishii for logistic support and H. Asano, K. Ono, and A. Okuda for identifying invertebrates and bird specimens. Financial support was provided by Japanese Ministry of Education, Science, Sport and Culture (grant nos. 09NP1501 and 11440224).

## Appendix

**Table 2** Bird species (names and abbreviations) observed during the study period

Abbreviation	Species	Total sightings	Focal species	Migration
FC	<i>Accipiter gularis</i> (Japanese Lesser Sparrowhawk)	3		S
LT	<i>Aegithalos caudatus</i> (Long-tailed Tit)	245	O	R
TP	<i>Anthus hodgsoni</i> (Olive-backed Tree Pipit)	132	O	S
OG	<i>Carduelis sinica</i> (Oriental Greenfinch)	43		S
SI	<i>Carduelis spinus</i> (Siskin)	3		R
TC	<i>Certhia familiaris</i> (Treetreeper)	349	O	R
JBW	<i>Cettia diphone</i> (Japanese Bush Warbler)	80		S
BW	<i>Cettia squameiceps</i> (Short-tailed Bush Warbler)	290	O	S
HF	<i>Coccothraustes coccothraustes</i> (Hawfinch)	22		S
CC	<i>Corvus macrorhynchos</i> (Jungle Crow)	15		R
OC	<i>Cuculus saturatus</i> (Oriental Cuckoo)	9		S
BWF	<i>Cyanoptila cyanomelana</i> (Blue and white Flycatcher)	122	O	S
BWP	<i>Dryocopus martius</i> (Black Woodpecker)	2		R
MB	<i>Emberiza cioides</i> (Siberian Meadow Bunting)	2		S
BFB	<i>Emberiza spdocephala</i> (Black-faced Bunting)	902	O	S
GB	<i>Emberiza variabilis</i> (Japanese Grey Bunting)	4		S
JG	<i>Eophona personata</i> (Japanese Grosbeak)	193		S
JR	<i>Erithacus akahige</i> (Japanese Robin)	3		S
SBR	<i>Erithacus cyane</i> (Siberian Blue Robin)	3		S
MF	<i>Erithacus cyanurus</i> (Red-flanked Bluetail)	8		S
NF	<i>Ficedula narcissina</i> (Narcissus Flycatcher)	859	O	S
JA	<i>Garrulus glandarius</i> (Jay)	28		R
BB	<i>Hypsipetes amaurotis</i> (Brown-eared Bulbul)	210		R
JPW	<i>Motacilla alba</i> (Pied Wagtail)	3		S
BF	<i>Muscicapa daurica</i> (Brown Flycatcher)	99	O	S
CT	<i>Parus ater</i> (Coal Tit)	551	O	R
GT	<i>Parus major</i> (Great Tit)	823	O	R
MT	<i>Parus palustris</i> (Marsh Tit)	871	O	R
VT	<i>Parus varius</i> (Varied Tit)	213	O	R
RS	<i>Passer rutilans</i> (Cinnamon Sparrow)	41		S
CW	<i>Phylloscopus coronatus</i> (Eastern Crowned Willow Warbler)	893	O	S
PWW	<i>Phylloscopus tenellipes</i> (Pale-legged Willow Warbler)	174	O	S
PWP	<i>Picoides kizuki</i> (Japanese Pigmy Woodpecker)	410	O	R
WWP	<i>Picoides leucotos</i> (White-backed Woodpecker)	28		R
GWP	<i>Picoides major</i> (Great Spotted Woodpecker)	197	O	R
GGW	<i>Picus canus</i> (Grey-headed Green Woodpecker)	6		R
BUF	<i>Pyrrhula pyrrhula</i> (Bullfinch)	25		W
GC	<i>Regulus regulus</i> (Goldcrest)	29		R
NH	<i>Sitta europea</i> (Nuthatch)	643	O	R
ST	<i>Sturnus cineraceus</i> (Grey Starling)	2		R
SS	<i>Sturnus philippensis</i> (Violet-backed Starling)	1		S
JGP	<i>Treron sieboldii</i> (Japanese Green Pigeon)	2		S
WR	<i>Troglodytes troglodytes</i> (Wren)	59		W
GTH	<i>Turdus cardis</i> (Japanese Grey Thrush)	454	O	S
BTH	<i>Turdus chrysolaus</i> (Red-bellied Thrush)	19		S
DTH	<i>Turdus naumanni</i> (Dusky Thrush)	14		W
WTH	<i>Zoothera dauma</i> (White's Thrush)	28		S
SGT	<i>Zoothera sibirica</i> (Siberian Ground Thrush)	1		S
WE	<i>Zosterops japonica</i> (Japanese White-eye)	9		S

Total sightings and migration behavior are indicated. Focal species used in analyses are indicated as O  
S summer migrants, W winter migrants, R residents

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