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Relative importance of the environmental factors at site and landscape scales for bats along the riparian zone

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Abstract To conserve and manage the bat population in an agricultural landscape, we investigated the relative importance of environmental factors on their occurrence and abundance in riparian zones at site and landscape scales. From May to October 2003, four bat species (*Myotis daubentonii*, *M. frater*, *Plecotus auritus*, and *Eptesicus nilssonii*) were mist-netted at 26 sampling sites in five streams in the Tokachi plain in central Hokkaido, northern Japan. The environmental factors of the two scales were measured at each sampling site. To clarify the most suitable landscape scale for bats, we also compared three spatial extents (250, 500, and 750 m) at each site. Generalized linear mixed models revealed that the occurrence and/or abundance of all four species, except for *M. frater*, was positively correlated with the percent cover of broadleaved deciduous forest and the height of bank-side tree canopy. Additionally, according to variation partitioning, although the value of the pure effect varied among species and measurement types, the site scale had a relatively larger pure effect than the landscape scale in many cases. However, in three of the five combined models, the proportion of confounding effect was much larger than that of the pure effect at the respective scales. Our study demonstrated that streams adjacent to a well-developed broadleaved deciduous forest are important for night habitats of many bat species in an agricultural landscape. Although focusing on the site scale may be important for bat conservation, we strongly stress the necessity for conservation and management plans at multiple scales.

Keywords Agricultural landscape · Variation partitioning · Multiple spatial scales · Stream · Forest · Conservation

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Introduction

The riparian zone, an interface between aquatic and terrestrial systems, harbors a wide variety of animal species (Gregory et al. 1991; Knopf et al. 1988; Naiman et al. 1993), and many of them are riparian specialists (Sabo et al. 2005). Despite their important role in maintaining regional biodiversity, riparian zones are severely degraded by human activities, including damming, river channelization, and human recreation (Brookes 1988; Miller et al. 2003; Rood et al. 1995; Scott et al. 2003). These habitat degradations are particularly serious in agricultural landscapes (Belanger and Grenier 2002; Nakamura and Yamada 2005; O'Neill et al. 1988). Therefore, conservation and management of the riparian zone is important for maintaining biological diversity in agricultural landscapes (Jobin et al. 2004).

The distribution of an organism is influenced by environmental factors that act at multiple spatial scales (Steffan-Dewenter et al. 2002; Thogmartin and Knutson 2007). These previous studies also indicate that evaluation of environmental factors at inappropriate spatial scales may provide

insufficient information for management, and stressed the importance of the evaluation of the responsible environmental factors at multiple scales. At the same time, habitat selection by animals is influenced by environmental factors that operate at multiple spatial scales (Fletcher and Hutto 2008; Okland et al. 2006). Thus, clarifying the relative importance of environmental factors on each scale provides important bases for determining the allocation of conservation resources at the appropriate scale (Fletcher and Hutto 2008). Moreover, because environmental requirement of animals can vary depend on their abundance and occurrence (Heinanen et al. 2008), conservation planning should consider these differences. Because the riparian zone harbors a wide variety of animals, and different species or taxa respond differently to environmental conditions, preferable conditions for the habitat should be evaluated according to multiple taxa. However, although many mammalian species are considered to prefer the riparian zone (i.e., Helfield and Naiman 2006; Maisonneuve and Rioux 2001; Sepulveda et al. 2007), limited studies have focused on terrestrial mammals. Bats, relatively well-studied riparian-dwelling mammals, are one of the largest taxa, which accounts for a quarter of the whole mammalian species (Kunz and Fenton 2003). Bats are also bioindicators in various habitats, particularly in agricultural landscapes (Jones et al. 2009): they show wide geographic ranges, gradual responses to habitat degradation correlated with responses of other taxa (i.e., insects), rich trophic diversity, slow reproductive rates that can result in rapid population declines, and they are reservoirs of a wide range of emerging infectious diseases whose epidemiology may reflect environmental stress. Nevertheless, approximately 45% of bat species are on the verge of extinction, mostly because of anthropogenic disturbances (Hutson et al. 2001). Therefore, efficient conservation strategies are urgently required.

River and riparian habitats are some of the most important habitats for foraging, drinking, and commuting for a broad range of bat species throughout the world (Ciechanowski 2002; Holloway and Barclay 2000; Lloyd et al. 2006; Racey et al. 1998; Whitaker 2004). Therefore, protecting these aquatic–terrestrial interrelated ecosystems is a high priority for bat management and conservation (Fukui et al. 2006). The importance of the riparian habitat for bats has been studied from several perspectives (i.e., comparison of river and riparian habitats to others, stream channel morphology, quality of riparian vegetation, and so on; Akasaka et al. 2009b; Grindal et al. 1999; Ober and Hayes 2008). However, most of these previous studies on bats' habitat selections were conducted on the site scale, and landscape studies are limited, with very few multiple-scale studies (but see Ober and Hayes 2008).

In this study, to conserve the bat population in an agricultural landscape, we clarified the relative importance of environmental factors at the site scale and at the landscape scale in river and riparian habitats.

Materials and methods

Target bat species in this study

In this study, we focused on four bat species, *Myotis daubentonii*, *M. frater*, *Plecotus auritus*, and *Eptesicus nilssonii*, of which number of bats captured were large enough to analyze. Although *M. macrodactylus* was captured at eight sites, the captured sites belonged to only two streams. Therefore, we did not use *M. macrodactylus* for the further analyses. All four species except *M. frater* are widely distributed throughout Europe and Asia (Encarnacao et al. 2005; Maeda 2005a; Rydell 1993; Stebbings 1988). *M. daubentonii* gaffs prey from the water surface (trawling species; Ciechanowski 2002). Because *M. daubentonii* forages almost dominantly in aquatic habitats (Kalko and Schnitzler 1989), this species may be sensitive to river and riparian alterations. The common and critical component of their diet is Diptera, especially adults and larvae of Chironomidae, although the diet differs among sites (Boonman et al. 1998; Flavin et al. 2001; Vaughan 1997). In contrast to *M. daubentonii*, although *M. frater* are found in Russia and Asia, there are few observations, and captured records of this species are from Asia only (Endo 1967; Kawai 2006; Kondo 2005). These reports state that *M. frater* is able to use a broad variety of habitats, ranging from natural to human. However, most of the biology of this species is unknown. *P. auritus* is one of the true forest species that gleans; they predominantly forage and roost in forests and take surface-bound prey from the ground or the vegetation (Anderson and Racey 1991). This species can fly slowly and hover, and they forage in forests relatively near the roost (within about 1.5 m; Entwistle et al. 1996). Their main diet is composed of Lepidoptera and Diptera (Vaughan 1997). *E. nilssonii* has been suggested as an opportunist for the foraging habitat; they prefer various types of open areas, such as forest edges, areas above the forest, farmland, parks with trees, streams and lakes, and street lamps (Dejong 1994; Rydell 1990, 1992, 1993; Wermundsen and Siivonen 2008). The diet of the species is composed of Diptera, mainly Chironomidae, Lepidoptera, Heteroptera, Aphidomorpha, and Psyllomorpha (Gajdosik and Gaisler 2004).

Study site

The study was conducted at five small streams in the Tokachi plain in central Hokkaido, northern Japan. All stream widths ranged from 2 to 7 m and lengths from 4 to 15 km.

Table 1 Explanatory variables considered in the analysis of bat occurrence and abundance at streams

Scale/variable	Unit	Description
Site scale		
Presence of bank-side trees		Presence of bank-side tree forming a continuous line (>5 m in length with no gaps) on either or both banks
Shelter's height	m	Average of maximum height of bank-side vegetation regardless of grass or tree among three measurement sites
Heights of bank-side tree canopy	m	Average of maximum height of bank-side tree canopy among three measurement sites
Volume of open space above stream	m^3	Volume of open area above water surface. The volume was calculated by the product of stream width at each measurement site, height from water surface to lowest tree cover (>30 cm thick) at each measurement site, and distance from upstream to downstream measurement site (20 m)
Landscape scale (within 250, 500, or 750 m)		
Road	%	Asphaltic, gravel, and earthen roads >3 m wide
Urban	%	Area such as town center, industry, and high- and low-density residential houses
Arable	%	Arable land and grassland in rotation horticultural land, and nonagricultural bare ground
Grassland	%	A range of grassland from permanent natural grassland to amenity grassland
Coniferous forest	%	Both seminatural and plantation conifer forest, having <30% of broadleaved trees in canopy
Broadleaved deciduous forest	%	All broadleaved forest such as ancient seminatural and plantation broadleaved forest, orchards, active coppice, and dense scrub
Water body	%	Running and standing water. In our study area, more than 97% of this land-cover type is stream

The Tokachi plain is one of the major agricultural areas of Japan. Although >95% of the land in the Tokachi plain was originally covered with broadleaved deciduous forest, most has been altered to arable land and pastures since the onset of settlement in 1883. The dominant tree species of the remnant forest are *Quercus dentate*, *Q. crispula*, *Betula platyphylla* var. *japonica*, and planted *Larix leptolepis*. The mean temperature was 6.4°C (maximum and minimum temperatures of 30.8°C and −22.5°C, respectively), and total precipitation was 830.5 mm in 2003 (data provided by the Obihiro Climatological Observatory located within the study area). During the research period, the mean daily temperature was 14.3°C (maximum and minimum temperatures 30.8°C and 0°C, respectively).

Bat capturing

We set 26 sampling sites in five streams (three to nine sampling sites in each stream). All sampling sites were located at least 1 km apart. Although bats may travel within a large area, the distance among each sampling site would not distort our result because Moran's I on the abundance and occurrence of the respective species was <0.05 and consistently not significant ($P > 0.05$). Bats were surveyed from May to October in 2003. We mist-netted each sampling site once every 2 months, or a total of three times. In each sampling site, three mist nets (each mist net was 2×6 m, with a 24-mm mesh size) were placed across streams for 2 h after sunset. We did not survey on rainy nights. Each capture was identified to

species according to Maeda (2005b). Although Kondo (2003) revealed clear identification of *M. gracilis* and *M. ikonnikovi*, it was difficult to identify these two species in our study periods (in 2003). Thus, we grouped these two species as *Myotis* spp.

Measurements of environmental factors

Environmental factors to explain the occurrence and abundance of bats were measured at site and landscape scales. We measured five site-scale environmental factors (stream width, presence of bank-side trees, shelter's height, height of bank-side tree canopy, and volume of open space above stream) in each sampling site (Table 1). Every site scale environmental factor except the presence of bank-side trees was measured at the mist-netted points and those 10 m downstream and upstream. Although habitat uses of some of bats were affected by water-surface conditions, there were few rapid-surface areas, which the bats would avoid in our sampling sites. Thus, we did not measure water-surface conditions. On the landscape scale, we used the percentage cover of land-cover types as predictive environmental factors. Because there was no clear evidence to determine the occurrence and abundance of bats on the landscape scale, we applied three spatial extents (250, 500, and 750 m) as the landscape scale according to Akasaka et al. (2009a; Fig. 1). We used digital land-use maps and a geographical information system (GIS, ArcGIS9.2; ESRI, Redlands, CA, USA) to determine the percentage cover of the land-use types for areas within three selected extents
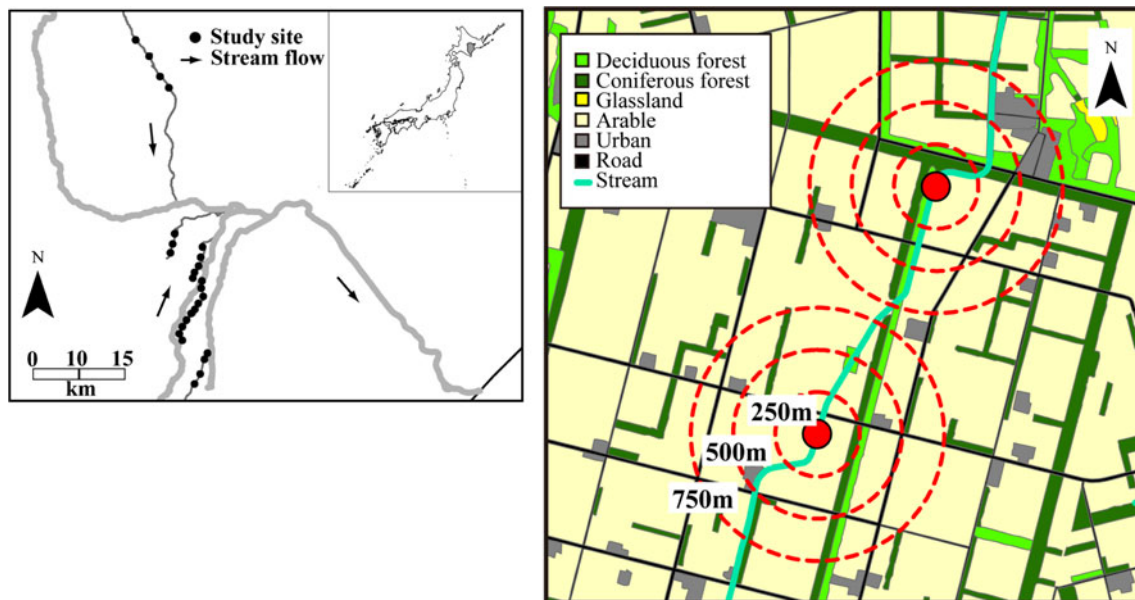
Fig. 1 Study area (in *gray*) within the Tokachi plain, Japan, and the diagram of each of the three spatial extents

from the sampling sites. Every sampling site was located by a hand-held Garmin WAAS-enabled Foretrex 101 GPS unit (Garmin International, Olathe, KS, USA) and plotted onto the digital land-cover map using the GIS. The land-cover types included Road, Urban, Arable, Grassland, Coniferous forest, Broadleaved deciduous forest, and Water body. The original land-use map was obtained from the latest vegetation/land-use map (scale of 1:25,000) on the Japan Integrated Biodiversity Information System (J-IBIS; Ministry of the Environment, 2000) and the National Spatial Data Infrastructure (Geographical Survey Institute, Government of Japan).

Data analysis

Factors determining the occurrence of bats

To clarify the relative importance of environmental factors on the sites and landscape scales to determine the occurrence of bats, we built three generalized linear mixed models (GLMM; Crawley 2002) based on three hypotheses. Firstly, we built a model based on the hypothesis that a bat occurrence can be explained only by site-scale environmental factors (site model). The explanatory variables were the five environmental factors measured (Table 1). The response variable was the presence or absence (1/0) of the bat in each sampling site. We used binomial error distribution and the logit link function and adopted a unique identification (ID) for each stream as a random effect for all the GLMM to model bat occurrence.

Site-scale environmental factors that best explained bat occurrences were selected by a best-subset selection procedure (Burnham and Anderson 1998) based on Akaike's Information Criterion (AIC). The model with the lowest AIC value was regarded as the best model. Secondly, a GLMM based on the hypothesis that bat occurrences can be explained only by landscape-scale environmental factors (landscape model) was built. The explanatory variables were percent covers of urban, arable, grassland, coniferous forest, and broadleaved deciduous forests within three spatial extents (250, 500, and 750 m) from each sampling site (Table 1). Because we did not use percent cover of road and water body as an explanatory variable, the sum of the percent cover of five land-cover type adopted was <100%. There was no significant correlation among each land-cover type ($r < 0.5$). The explanatory variable of each model was composed of one spatial extent variable. Thirdly, a GLMM based on the hypothesis that bat occurrences can be explained by both site- and landscape-scale environmental factors was built (combined model). We used the best predictive variables of both site and landscape models as explanatory variables of the combined model.

To reveal the relative importance of environmental factors in the two scales on bat occurrence, the pure effect of site and landscape environmental factors were respectively calculated by variation partitioning (Borcard et al. 1992; Meot et al. 1998) using the three above-mentioned models (site, landscape, and combined model). Variation partitioning can evaluate the relative importance among several groups of predictive variables on the same response

variable. The pure effect of environmental factors on the respective scale was calculated by the following fractions, where "L" is the contribution of the landscape-scale model, "S" is the contribution of site-scale model, "C" is the contribution of the combined model, "a" is the pure effect of the site-scale model, "b" is the pure effect of the landscape-scale model, and "d" is the confounding effect of the site and landscape model.

$$d = (L + S) - C$$
$$a = L - d$$
$$b = S - d$$

When the confounding was calculated to be negative, the value is treated as zero. The contribution of each model was calculated as the percentage deviance explained [100 × (null deviance − residual deviance)/null deviance] (see Dobson 1999). All site-scale environmental factors, except for the presence of bank-side trees, were log-transformed, and all landscape factors were arcsine-transformed. We excluded arable land cover from the landscape-scale analysis on *P. auritus* because *P. auritus* obviously did not use this land-cover type, and inclusion of this factor led to nonconvergence of the model. All statistical analyses were conducted using the statistical package R version 2.9.2 (R Development Core Team, 2008).

Factors determining the abundance of bats

We determined the environmental factors and their relative importance at two scales (site and landscape scales) that best explained the abundance of each bat species by the same procedures as the bat occurrence. In the analyses on abundance, we used only the sampling sites in which the respective bat species were present. The response variables were the abundance of bats in each sampling site. We used the highest number of the three captures at each sampling site. We used a Poisson error distribution and a log-link function and adopted a unique ID for each stream as the random effect for all GLMM in the abundance models. We did not use the percentage cover of arable land in the landscape scale analysis for *P. auritus* as the model on occurrence. We excluded *E. nilssonii* from the analysis due to the small number of observed sites.

Results

We caught 293 individuals from seven species belonging to four genera (Table 2). Regarding the target species, we caught 116 *M. daubentonii* in 12 sites, 48 *M. frater* in nine sites, 43 *P. auritus* in eight sites, and 16 *E. nilsonii* in eight sites.

Factors determining the occurrence of bats

The occurrence of each bat species was explained by different environmental factors, whereas the most relevant spatial extent at the landscape scale was 750 m for all four species. On the site scale, the height of bank-side tree canopy was the best predictor explaining the occurrence of *M. daubentonii* (Table 3). *M. daubentonii* was likely to occur where the bank-side tree canopy was high. On the other hand, the best model of the landscape scale was positively correlated with the cover of broadleaved deciduous forest and negatively correlated with the urban cover (Table 3). The three models of *M. daubentonii* (best model of site and landscape models and the combined model) explained 43.25, 29.82, and 56.61% of the total deviation, respectively. Confounding in the two scales was 16.46% (Fig. 2), and the pure effect of each of the two scales was 26.79% (for the site scale) and 13.36% (for the landscape scale). The occurrence of *M. frater* was not related to any environmental factors in either scale. For *P. auritus*, both bank-side tree canopy at the site scale (deviance explained 8.50%) and percentage cover of broadleaved deciduous forest on the landscape scale (deviance explained 40.64%) were positively correlated with their occurrence (Table 3). The combined model of the *P. auritus* occurrence explained 49.14% of the total deviation, and confounding of the two scales was 0%, indicating that the pure effect of each of the two scales in this species was completely independent (Fig. 2). Although *E. nilssonii* did not correlate with any site-scale environmental factor, all land cover was positively correlated with the occurrence of this species (deviance explained 86.19%).

Factors determining the abundance of bats

Each bat species was related to a variety of environmental factors at both spatial scales. The abundance of *M. daubentonii* was best explained by the height of bank-side tree canopy at the site scale and the percentage cover of broadleaved deciduous forest within 250 m of spatial extent at the landscape scale (Table 3). Both variables were positively correlated with abundance (Table 3). The percentage deviance explained for each scale model and the combined model was 57.19% (site scale), 63.26% (landscape scale), and 63.61% (combined). Thus, confounding accounted for a greater percentage (56.84%) than the pure effect of the two scales (site scale 0.35%, landscape scale 6.42%; Fig. 2). The abundance of *M. frater* was not related to any of the environmental factors on the two scales. The abundance of *P. auritus* increased in the site with wide, open space above the stream (site-scale deviance explained 44.01%) and the low percentage cover of grassland (landscape-scale 500 m spatial extent; deviance explained 27.93%; Table 3). Deviance explained by the combined

Table 2 Number of captured bats in 26 sampling sites

Species	Number of captures		Number of captured sites
	Total	Mean ± standard deviation	
M. daubentonii	116	23.2 ± 25.7	12
M. frater	48	9.6 ± 6.54	9
M. macrodactylus	14	2.8 ± 4.66	8
M. spp.	45	9 ± 11.4	9
P. auritus	43	8.6 ± 11.8	8
M. ussuriensis	4	0.8 ± 0.8	3
M. hilgendorfi	7	1.4 ± 19.5	5
E. nilssonii	16	3.2 ± 3.2	8

Table 3 Final selected models and Akaike's Information Criterion (AIC) explaining abundance and occurrence of each bat species at the two scales (site and landscape)

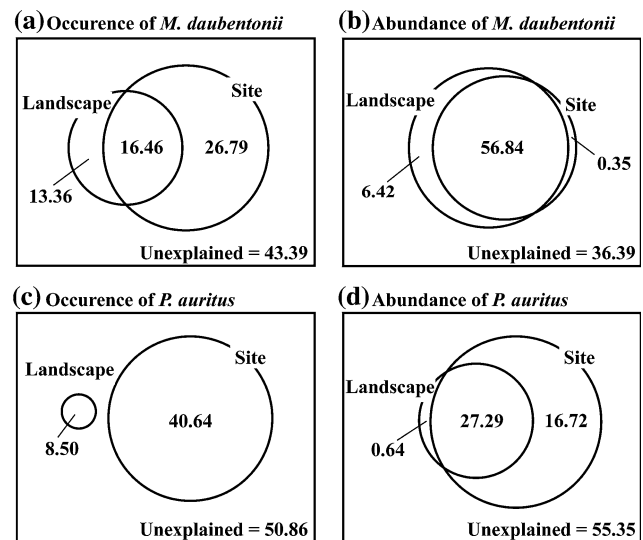| Spatial scale	Model formula
M. daubentonii	
Occurrence	
Site	+ Height of bank-side tree canopy
Landscape (750 m)	− Urban + broadleaved deciduous forest
Abundance	
Site	+ Height of bank-side tree canopy
Landscape (250 m)	+ Broadleaved deciduous forest
P. auritus	
Occurrence	
Site	+ Height of bank-side tree canopy
Landscape (750 m)	+ Broadleaved deciduous forest
Abundance	
Site	+ Volume of open space above the stream
Landscape (500 m)	− Grassland
E. nilssonii	
Occurrence	
Site	NULL
Landscape (750 m)	+ Urban + arable + grassland + broadleaved deciduous forest + coniferous forest

Null model was selected as best model for both occurrence and abundance of *M. frater* in both scales

Fig. 2 Venn diagram showing the variation explained (%: percent deviance explained) at site and landscape scales on habitat selection by bats. Note that ellipse sizes do not scale with the variation explained

more than one land-cover type for the landscape model (Table 3). Although previous studies often used either occurrence or abundance of the organisms to evaluate the suitable scale for preferable habitats (i.e., Bowman et al. 2001; Smith et al. 2008; Warren et al. 2005), their results were hardly distinguished from one another. Our results pointed out the need for clear discrimination of the measurements used and the importance of conducting assessments by both measurements when planning conservation programs. The selected spatial extent of the occurrence of *M. daubentonii* and *P. auritus*, of which the best model of both sites and landscape models included more than one environmental factor, was smaller than that of the abundance. Additionally, the site scale had a relatively larger pure effect than the landscape scale in many cases, although the volume of the pure effect varied among species and type of measurement. Habitat selection by bats could emphasize fine-scale selection of sites within a home range (Johnson 1980; Ober and Hayes 2008) because bats, similarly to birds, can exploit geographically disjunct habitat patches due to high mobility and relatively low energy costs during flight. These previous studies support our results, and our data also suggest that abundance, which provides more detailed information on habitat selection, is influenced more by a finer spatial extent than occurrence.

The models of three out of the five species focused their explanatory power on incorporating environmental factors on both site and landscape scales. This suggests that the distribution of bats is often influenced by environmental factors on at least two spatial scales. However, in three out of the five combined models, the proportion of the

model was 44.65%. Confounding and the pure effect of site and landscape scales was 27.29, 16.7, and 0.64%, respectively (Fig. 2).

Discussion

Relative importance of site and landscape scales

The most suitable spatial extent for occurrence and abundance differed in all three bat species, which was related to

confounding effect was much larger than that of the pure effect of the respective scales (Fig. 2; Table 3). The large volume of the confounding effect that represents the interscale effect indicates that environmental factors on multiple scales interactively influence bat distribution, suggesting that a conservation program should take multiple scales into account (Fletcher and Hutto 2008; Nakamura et al. 2005).

Habitat preference of bats

The percent cover of broadleaved deciduous forest was positively correlated with at least the occurrence or the abundance of all of bat species, except for *M. frater* (Table 3). Our results were in line with studies that showed the preference of bats for streams that run through a broadleaved deciduous forest (Holloway and Barclay 2000; Lloyd et al. 2006). Both types of habitats are important for both aquatic and terrestrial insects, and these habitats harbor large quantities and diverse species of insects (Fukui et al. 2006). Broadleaved deciduous forests also provide safe sites against predators and wind (Russ and Montgomery 2002). Likewise, on the site scale, bats prefer a liner edge structure, especially the river–riparian forest ecotone, for commuting corridors and foraging ground (Verboom and Spoelstra 1999; Warren et al. 2000). Therefore, many bat species, including our target species, prefer streams surrounded by large areas of broadleaved deciduous forests and that have well-grown bank-side trees.

The percent cover of the broadleaved deciduous forest and the height of bank-side tree canopy were positively correlated to both occurrence and abundance of *M. daubentonii* (Table 3). Well-grown bank-side trees are important for foraging because *M. daubentonii* are a wind-sensitive species (Russo and Jones 2003). Because all previous studies on habitat selection of *M. daubentonii* were conducted on the site scale, our study is the first to clarify the positive association of *M. daubentonii* and the surrounding forest cover at the landscape scale and to delineate a relevant landscape extent within which the land-cover component influences the habitat selection of this species. *M. daubentonii* dominantly forages along the river; however, this species uses the forest under the cold, windy condition because insects are more abundant in the forest than above the stream under this condition (Vaughan et al. 1997). Moreover, to reduce predation risks, this species also forages inside the forest at dusk (Nyholm 1965). Because our survey period was 2 h after sunset, this period included dusk and evening twilight time. Therefore, we suggest that the stream surrounded by forest provides benefits for foraging. The negative association between *M. daubentonii* and urban land cover may be the consequence of the loss of forest.

The occurrence of *P. auritus* showed a positive correlation to the percent cover of the broadleaved deciduous forest and the height of the bank-side tree canopy (Table 3). Because *P. auritus* predominantly forages in forests, it is a true forest species and its echolocation structure and wing shape are well-adapted to forests (Norberg and Rayner 1987), which allows slow and maneuverable flights (including hovering). The well-developed broadleaved deciduous forest provides many surfaces from which the species can glean insects (Entwistle et al. 1996). Additionally, *P. auritus* uses linear features, such as edges of tree lines (i.e., hedgerow and rides through forests) and hedges for commuting routes between feeding sites (Entwistle et al. 1996). Consequently, we inferred that well-developed bank-side trees adjacent to the stream and the surrounding forests are preferred as a commuting site. Within forests, *P. auritus* was abundant in the wide, open area above a stream, with a low percentage of grassland cover. Open space, such as grassland, increases predation risk, especially for slow-flying bats (Entwistle et al. 1996). Additionally, the abundance of Lepidoptera, which is the main diet component for *P. auritus*, is very low in grasslands (Entwistle et al. 1996). These high risks of predation and low prey resources for *P. auritus* in the grassland seem to result in the negative relation between *P. auritus* and the proportion of grassland cover (Table 3). Although we are not able to find the reason for the correlation between bat abundance and the volume of open space above water from previously published studies, because *P. auritus* uses linear open space with trees for commuting (Entwistle et al. 1996), the correlation may be related to the commuting habitat.

The occurrence of *E. nilssonii* was not correlated with any site-scale environmental factors, but it was correlated with all factors on the landscape scale, including the percentage of cover of the broadleaved deciduous forest. This species uses a variety of habitat flexibly and, thus, is thought to be opportunist in night habitats (Haupt et al. 2006; Wermundsen and Siivonen 2008). Our results support these previous studies and suggest that *E. nilssonii* can forage extensively in this study area. In turn, both the occurrence and abundance of *M. frater* did not correlate with any environmental factors. *M. frater* has been observed in a wide range of habitats, such as around street lamps, above and surrounding houses, on arable land, and in forests (Endo 1967; Kawai 2006; Kondo 2005). We also suggest that *M. frater* is a generalist in the night habitat.

Conclusions and implications

Our study demonstrated that streams with adjacent well-developed broadleaved deciduous forests are important for the night habitats of many bat species in agricultural

landscapes, although the underlying mechanisms are different among species. Although attention to site scale may be relatively important for bat conservation, we strongly emphasize the necessity for conservation and management plans to work on a multiple scale. In this study, we did not handle the explicit factors that indicate anthropogenic disturbances. However, the low percentage of cover of broadleaved deciduous forests can be interpreted as a high percentage of human-mediated land cover, because >95% of the study area was covered by broadleaved deciduous forests before settlement and development began in 1883 (Kikuchi 2002). In that sense, our results not only contribute to deepening the understanding of the mechanism that determines bat community but also provide valuable information on the degree to which the forthcoming anthropogenic forest plantation will damage bat communities. Using statistical models such as the ones we developed, a systematic a priori assessment of the impact of forest degradation, and assessment of the efficiency of conservation and management plans, are required when taking environmental factors into account on multiple spatial scales.

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