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Patterns of resource use in an assemblage of birds in the canopy of a temperate alluvial forest

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Abstract In our study, we assessed patterns of resource use in an assemblage of birds by observing their foraging behaviour from a crane in the canopy of a temperate alluvial forest. We selected 12 bird species and addressed seasonal changes in feeding activity during a 2-month period in spring focussing on average staying time and utilisation of crown strata in two tree species, the common oak (*Quercus robur*) and the sycamore maple (*Acer pseudoplatanus*). We further examined ecological characteristics of the trees (i. e., crown density) that are likely to influence resource use in birds. The selected birds differed in their preference for the tree species. Most birds preferred common oaks. This preference was probably associated with higher food abundance related to substrate characteristics (i.e., roughness of bark) which offer more microhabitats for arthropods and thus permit higher densities of potential prey. Some bird species switched feeding preferences within the study period from sycamore maples to common oaks in association with tree phenology. We found two main foraging techniques. All birds searched for prey at short distance (≤50 cm) and gleaned food from substrate except the Pied Flycatcher that foraged by hovering and searched over longer distances (>50 cm). Overall, we demonstrate in our study that canopy access with mobile crane systems provides excellent opportunities to observe canopy birds and enables detailed analysis of their foraging behaviour. The main result of our study reveals fine-grained resource partitioning of birds within the canopy as an important factor structuring assemblages, with species-specific and in part also seasonal differences in stratification and substrate use.

Keywords Foraging technique · *Acer* · *Quercus* · Niche partitioning · Stratification

Introduction

A better understanding of resource use in relation to structural components as well as availability and distribution of food is central to the study of community organisation of birds (Rosenberg 1990). Birds like all other organisms have to adapt to local habitat and resource conditions to satisfy their energy demands. Each individual has to decide which habitats or patches should be visited more often than others to cover its daily energy budget (Holmes et al. 1979; Dunning 1990; Moermond 1990; Davison and Jones 1997). Those decisions are particularly important for syntopic bird species that use similar resources. In this context, resource partitioning has been acknowledged as an important factor structuring local bird assemblages where differences in morphological, physiological, and behavioural characteristics result in differential resource use including differences in foraging strategies (Robinson and Holmes 1982; Holmes and Robinson 1988; Salewski et al. 2003) and stratification patterns (Greenberg 1981; Walther 2002; Utschick 2006). Furthermore, as food availability is often strongly seasonal (Hejl and Verner

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1990), birds respond to the spatial and temporal availability of resources with a specialised or a more generalised foraging behaviour.

Species diversity and composition of bird assemblages are strongly associated with structural parameters. Activity of forest birds, for example, is largely influenced by volume and height of the forests as well as by the amount of dead wood (e.g. Miranda and Pasinelli 2001; Naka 2003; Lehmann 2004; Utschick 2006). Observed differences in resource use of birds are attributed at least in part to the composition and availability of arthropods (Mariani and Manuwal 1990). For example, tall trees with thick trunks, structured bark and high crown volumes as well as a large amount of dead wood harbour more arthropods than smaller trees with plain bark and hence fewer microhabitats (Lehmann 2004).

Studies on resource use of birds suggest a prominent role of the canopy for species richness and abundance as it represents, for many forest-dwelling species, the most important habitat for courtship, establishment and defence of territories, nest building, and as substrate for foraging (e.g. Utschick 2006). However, in spite of its importance for species diversity, there are only very few studies on canopy use by birds (e.g. Shaw et al. 2002; Utschick 2006). One of the main reasons is the difficulty of conducting behavioural observations of birds in the canopy from the ground (Walther 2003). So far, most studies on canopy use by birds have been conducted in the tropics (i.e. Canopy crane project in Fort Sherman and Parque Metropolitano, Panama: Wright 2002; Van Bael and Brawn 2005; Surumoni Crane Project: Venezuela, Winkler and Listabarth 2003) and only very few in temperate forests (Wind River Crane System, USA: Shaw et al. 2003). In 2001, a mobile canopy crane was installed in an alluvial forest near the city of Leipzig, Germany, with a gondola navigable in three dimensions. The "Leipziger Auwaldkran-Projekt" (LAK) aims at investigating species composition, interactions and functionality of selected taxa in a comprehensive approach (Morawetz and Horchler 2003).

In our study, we analysed and compared patterns of resource use of birds in the canopy of two common tree species, the common oak (*Quercus robur*) and the sycamore maple (*Acer pseudoplatanus*). Both species are native and typical for the area. Overall, our primary objective was to assess species composition of forest birds and to compare patterns of resource use during the main growing season of the vegetation in spring. We asked whether bird species differ in their preference of trees and in their foraging behaviour. Thereby, we assumed that birds should favour those foraging areas in which they can satisfy their daily energy demands rapidly. Hence, we expected that the observed bird species should favour *Quercus* because of the higher abundance of arthropods (Nicolai 1985; Lehmann 2004). We further assumed that the birds adapt to changes in prey availability during the main growing season by shifting their feeding preferences in relation to distinct differences in phenology between *Quercus* and *Acer*. Furthermore, we proposed that co-existing, ecologically and morphologically similar species should show species-specific preferences for selected spaces within the crowns to reduce potential overlap in resource use.

Methods

Study area

The study took place in the northern part of the alluvial forest of Leipzig, called Burgaue, in the catchment area of the rivers Luppe and Weiße Elster at an altitude of 120 m a.s.l. Annual rainfall is low (515 mm) compared to the mean rainfall for Germany (700 mm). Average yearly temperature is about 9.5°C (Tal, Botanical Institute, Leipzig, personal communication). The forest was officially declared as a nature reserve in 1912 and covers an expanse of 270 ha. The crane site is located in the eastern part of the nature reserve. The crane has been installed on a 120-m-long railway that divides the crane plot into two sections. The western area is part of the nature reserve; the eastern part consists of a transition zone between forest and shrubs. The crane (Liebherr, Type 71 EC) is 40 m tall and covers a total area of about 1.6 ha including the railway and a 45-m-long boom.

Until the early twentieth century the vegetation of the study area represented a typical floodplain forest of the Querco-Ulmetum-zone (Morawetz and Horchler 2003). Subsequently, lowering of the ground water level by human activities lead to changes in the composition of tree species, favouring the sycamore maple which represents today the most common tree species in the crane plot (Morawetz and Horchler 2003). Currently, the forest stand at the crane site is characterised by 17 tree species that differ in abundance. The most common tree species (stem diameter at breast height: DBH $\geq$5 cm) in the study area are sycamore maple ($n = 226$), followed by common ash (*Fraxinus excelsior*; $n = 111$), small-leaved linden (*Tilia cordata*; $n = 219$), Norway maple (*Acer platanoides*; $n = 154$), smooth-leaved elm (*Ulmus cf. minor*; $n = 93$), common hornbeam (*Carpinus betulus*; $n = 67$), and common oak ($n = 15$). Individual common oaks represent the oldest trees in the crane plot with an age of more than 240 years (Morawetz and Horchler 2003).

Collection of vegetative data

We selected two common tree species, the common oak and the sycamore maple, for our observations. Both differ in flowering period, leaf flush and timing of fruit production. We grouped several trees per species into six observation groups (1–4 tree individuals per group; Fig. 1). This gave us the opportunity to observe several trees at the same time. Although individual trees varied in size, each group had a similar crown volume to permit standardised comparison of tree use by the birds. In addition, we assessed several vegetation parameters to analyse their potential influence on bird foraging behaviour. Those included tree height, crown volume, foliage density, amount of dead wood, density of tree stand and DBH. The volume of the crowns was calculated with different models (cylinder, cone, neiloid or paraboloid) depending on their shape (Nilson 1999). To assess foliage density, we followed Bibby et al. (1995) and adopted the checkerboard method of recording vertical density of the shrub layer (size of checkerboard: 50 × 50 cm with 10 × 10 cm squares). Furthermore, we recorded the volume of dead wood for each tree crown by adding up the length of each dead branch and by multiplying the total length of the dead branches with the diameter of the twigs taking a cylindrical barrel as a model. Additionally, we also characterised the density of the tree stand by estimating the degree of overlap in twigs of each selected tree with its neighbours.

Finally, the canopy area of each tree was divided equally along the vertical axis into upper, middle and lower crown. Subsequently, each of the vertical crown sections was then divided horizontally into equal parts in relation to the stem into outside, middle and inside beginning with the outermost twigs until the inside of the crown (Fig. 2). We further noted structural characteristics, such as tree hollows in the trunk or broken-off branches to pinpoint the transition between the zones.

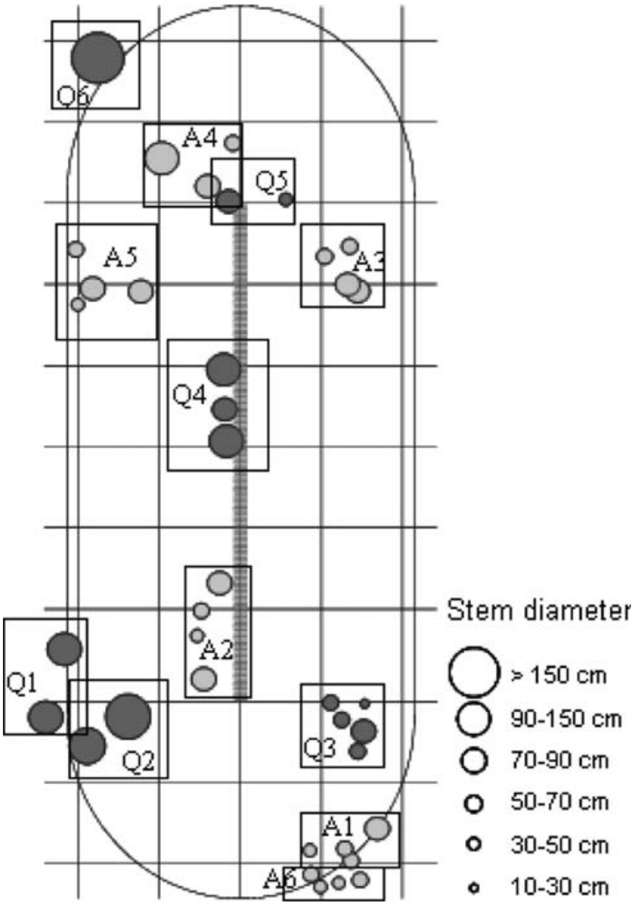

Fig. 1 Selected tree individuals in the crane plot (grid system (20 × 20 m) follows Morawetz and Horchler (2003). *Black circles* selected common oaks (*Quercus robur*), *grey circles* selected sycamore maples (*Acer pseudoplatanus*); the *rectangles* describe the particular patches selected for each tree species with patch identification number (Q = *Quercus robur*; A = *Acer pseudoplatanus*)

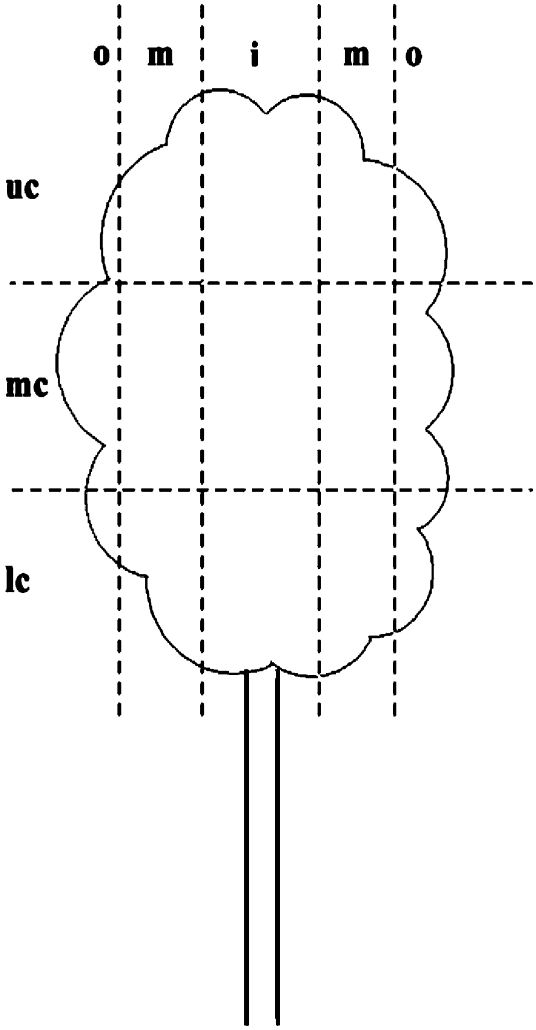

Fig. 2 Classification of a tree crown into different strata; vertical dimension: *uc* upper crown, *mc* middle crown, *lc* lower crown; horizontal dimension: *o* outside, *m* middle, *i* inside

Bird census techniques

Observations of foraging birds in the alluvial forest took place from 4 April to 28 May 2005 (first week: 4–8 April, second week: 11–15 April, third week: 18–23 April, fourth week: 25–29 April, fifth week: 2–6 May, sixth week: 9–13 May, seventh week: 16–20 May, eighth week: 23–27 May). We checked the 12 tree groups 3 days per week, spending 45 min each per group, and changing the sequence of the observed groups daily. Overall, each tree was observed three times per week during the 2-month study period.

Birds were observed continuously in the canopy where one observation refers to one visit of a bird as long as it stayed in one of the studied tree crowns. All observations were recorded immediately onto a Dictaphone (microcassette-corder M-730V, Sony microcassette MC-60). We documented bird species, patch and tree number, stratum, height of the bird above ground, duration of its stay, foraging strategy, foraging substrate and searching activities. We estimated the height of the foraging bird above the forest floor to calculate the foraging-height-index (=height of bird above ground/height of tree; Nyström 1991). This index permits assessment of possible height preferences of bird species within trees and potential changes in relation to vegetation period or other factors.

We differentiated whether a bird searched for prey or actually captured food. Foraging behaviour was divided into five categories. The category "glean" describes a bird taking food from substrate including twigs, trunk, leaves (underside, upper side, and petiole) or flowers. The category "jump" includes all directed jumps of a bird from a twig towards insects on leaves or flowers without flapping its wings. In contrast, the category "probe" comprises all undirected activities of a bird, which are connected with foraging behaviour, for example hacking on a twig or turning a leaf or flower. "Aerial-glean" describes a bird's attempt to catch prey by hovering in front of substrate like leaves or twigs. The category "aerial" implies hunting in the air in the flycatcher style, i.e. starting from a branch, flying directly towards moving prey and catching it in mid-air (Robinson and Holmes 1982; Salewski et al. 2002). Furthermore, we recorded foraging substrate and differentiated between lower and upper surface of the leaves, wood (including branches and trunks) and air.

As noted above, we also recorded searching activities of the birds in addition to foraging sequences. When a bird changed its position, we estimated the distance moved and subsequently classified it into "short-distance-searcher" ($\leq$50 cm) or "long-distance-searcher" (>50 cm) following Robinson and Holmes (1982).

We pooled search and foraging rates of each bird species that had been observed during our study period in a tree crown and related its activities to the vegetation period by addressing potential changes in the ratio of searching and foraging behaviour for the respective species. Foraging sequences were defined as periods where the birds continued to capture prey items and searching sequences as the time of all searching movements without any immediate prey attack. For each stay of a bird in a tree crown, we tallied the number of observations showing direct evidence of foraging or searching movements. This was divided by the number of seconds of the staying time to obtain a measure of foraging and search rate.

Statistics

For statistical analysis, the programs SigmaStat 3.1 and Statistica were used. We tested the data for normality and subsequently applied parametric (t test) or nonparametric tests (Mann–Whitney U test) depending on whether the data were normally distributed or not. To compare groups, we utilised the Kruskal–Wallis one-way analysis of variance on ranks (ANOVA on ranks: H test) and to compare distributions, we applied the chi-square test (χ^2). We used generalised linear models (GLMs) to describe preferences of birds for specific tree characteristics. Overall, we accepted $P \leq 0.05$ for all tests as the level of significance.

Results

We observed the foraging behaviour of 34 bird species in the crowns of common oaks and sycamore maples. From those, we selected a subset of 12 species for detailed analysis based on a minimum sample of $n = 10$ observations per species (Table 1).

Preference of tree species

The selected bird species showed an unequal distribution of their visits of common oaks and sycamore maple. Each bird species preferred one of the two trees for foraging although none of the species used one tree species exclusively. The difference in the number of visits between both tree species was significant for 9 of the 12 selected bird species which clearly preferred the common oak over the sycamore maple (Table 1). In the three remaining bird species, Great Spotted Woodpecker, Blackcap, and Great Tit (scientific names of all bird species are given in Table 1), the difference in the number of observations in the two tree species was not significant, suggesting that they had no strict preference.

Comparing the number of visits of the 12 bird species during the vegetation period revealed distinct differences in visitation rates of the crowns of common oak and sycamore maple in relation to flowering phenology and leaf age (Fig. 3). At the beginning of the observation period in the

Table 1 Preference of tree species of the 12 selected bird species given as % visits of common oak versus sycamore maple, total observation time and statistical comparison of % visits of the two tree species

Bird species	*n*	BP[ab]	Total observation time (min)	Visits common oak (%)	Visits sycamore maple (%)	Statistics
Blue Tit (*Cyanistes caeruleus*)	322	2 (8)	347.5	65.8	34.2	$t = 45.00$; $P = 0.046$
Great Tit (*Parus major*)	60	3 (7)	49.6	55.0	45.0	NS
Chaffinch (*Fringilla coelebs*)	34	2 (6)	32.3	70.6	29.4	$t = 76.00$; $P = 0.031$
Great Spotted Woodpecker (*Dendrocopos major*)	25	1 (3)	15.2	88.0	12.0	$t = 106.50$; $P = 0.013$
Middle Spotted Woodpecker (*Dendrocopos medius*)	21	1 (4)	48.3	42.9	57.1	NS
Lesser Spotted Woodpecker (*Dendrocopos minor*)	12	1 (4)	16.8	91.7	8.3	$t = 53.00$; $P = 0.005$
Blackcap (*Sylvia atricapilla*)	23	2 (4)	27.4	47.8	52.2	NS
Pied Flycatcher (*Ficedula hypoleuca*)	24	2 (3)	9.7	83.3	16.7	$t = 70.50$; $P = 0.01$
European Starling (*Sturnus vulgaris*)	70	3 (7)	33.9	81.7	18.3	$t = 45.50$; $P = 0.015$
Nuthatch (*Sitta europaea*)	39	2 (4)	25.9	94.9	5.1	$t = 117.00$; $P < 0.001$
Short-toed Treecreeper (*Certhia brachydactyla*)	15	1 (2)	10.3	93.3	6.7	$t = 63.00$; $P = 0.002$
Chiffchaff (*Phylloscopus collybita*)	10	1 (2)	27.4	87.5	12.5	$U = -2.78$; $P = 0.032$

NS Not significant

[a] *BP* Number of breeding pairs in the crane plot

[b] Maximum number of individuals which were observed simultaneously in tree tops of the study site shown in parentheses

first week of April, individuals of both tree species had produced thousands of buds. However, whereas the buds from the sycamore maple were fully developed at this time, those from the common oak were still premature. During this time, the birds favoured the crowns of common oaks with the premature buds over those of sycamore maples ($U = 35.50$; $P = 0.026$). In the second observation week, individual sycamore maples started to flower and produced leaves in contrast to the common oaks where flowering and leaf flush started 2 weeks later in the fourth week. In the second to fourth observation weeks, there was no significant difference between the utilisation of both tree species, which were visited equally often by the foraging birds. In the time period between 25 April and 6 May (fourth and fifth observation weeks), five bird species, which had mostly foraged in sycamore maples in April, switched to common oaks in May (Fig. 3). The focus on common oaks as the main foraging substrate in May was most pronounced in Great Tits ($\chi^2 = 19.25$; $df = 1$; $P \leq 0.001$), Blue Tits ($\chi^2 = 10.99$; $df = 1$; $P \leq 0.001$), Chaffinches ($\chi^2 = 6.92$; $df = 1$; $P = 0.009$), Blackcaps ($\chi^2 = 13.44$; $df = 1$; $P \leq 0.001$) and European Starlings ($\chi^2 = 11.78$; $df = 1$; $P \leq 0.001$).

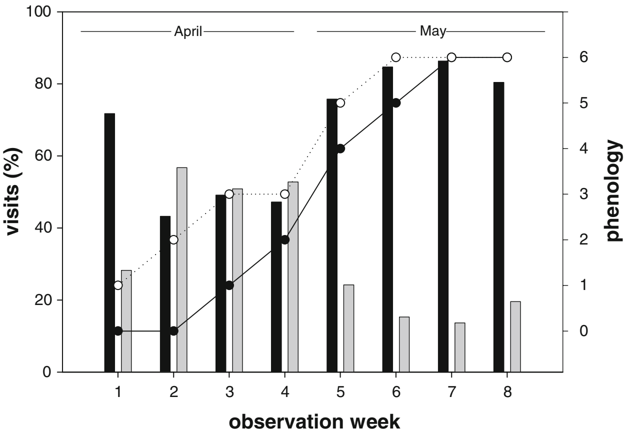

Fig. 3 Percentage of bird visits (*bars*) of the two tree species in relation to tree phenology (*lines*). *Black line* and *bars*: *Quercus robur*; *dotted line* and *grey bars*: *Acer pseudoplatanus*. Phenology: *0* closed buds, *1* buds with green apex, *2* opening of bud, *3* leaf unfurled by 25%, *4* leaf unfurled by 50%, *5* leaf unfurled by 75%, *6* leaf fully unfurled

Staying time in the tree crown

Some of the observed bird species differed in their average staying time per tree crown. The Middle Spotted Woodpecker ($t = 325.00$; $P < 0.001$), the Lesser Spotted Woodpecker ($t = 225.00$; $P = 0.019$), the Blue Tit ($t = 1495.00$; $P = 0.032$), and the Blackcap ($t = 335.00$; $P = 0.008$) stayed on average significantly longer in one tree top than the Pied Flycatcher. The difference in staying time of the other bird species was not significant. Blue Tits spent more time per tree visit in the canopy of sycamore maples than of common oaks ($t = 12561.00$; $P = 0.021$).

Table 2 Average staying time (s) in the canopy with standard deviation (SD) and weekly sampling during the observation period of the 12 selected bird species

Bird species[a]	Average ± SD	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8
Blue Tit (322)	83 ± 105	73	138	118	78	80	43	73	54
Great Tit (60)	66 ± 61	138	59	54	25	54	73	9	41
Chaffinch (34)	74 ± 87	–	12	130	63	–	122	70	37
Great Spotted Woodpecker (25)	53 ± 68	39	11	–	190	25	30	46	–
Middle Spotted Woodpecker (21)	193 ± 192	6	439	322	170	158	86	–	–
Lesser Spotted Woodpecker (12)	84 ± 62	–	12	130	63	–	122	70	37
Blackcap (23)	102 ± 119	–	113	195	33	–	27	109	49
Pied Flycatcher (24)	36 ± 37	–	–	15	23	37	30	44	–
European Starling (71)	55 ± 44	10	–	–	38	–	65	47	–
Nuthatch (39)	62 ± 53.8	28	52	33	60	37	57	129	92
Short-toed Treecreeper (15)	62 ± 80	30	23	8	24	20	79	139	–
Chiffchaff (10)	75 ± 76	–	–	–	–	–	45	136	–

[a] Sample size (number of observations per bird species) is given in parentheses

The other bird species showed no significant differences. The staying time of the birds per tree top changed in some species during the observation period (Table 2). Blue Tits foraged at the beginning of our data collection significantly longer in each tree crown than in the last weeks of May ($t = 9562.50$; $P \leq 0.001$). Great Tits, Blackcaps and Middle Spotted Woodpeckers showed the same trend like Blue Tits, but there was no significant difference between April and May. Some species, however, the Chaffinch, the Great Spotted Woodpecker, and the Lesser Spotted Woodpecker, showed similar staying times during the eight observation weeks. Furthermore, some species tended to prolong their staying time per tree crown throughout the study period, but these differences were not significant for the Pied Flycatcher, the European Starling, the Nuthatch, and the Short-toed Treecreeper (Table 2).

Vertical and horizontal stratification

We recorded spatial use within tree crowns for each of the 12 bird species to assess possible species-specific preferences of microhabitats. Comparing vertical and horizontal stratification of birds between common oaks and sycamore maples revealed similar results: there was no significant difference in the stratification patterns of birds in both tree species ($\chi^2 = 56.00$; $df = 48$; $P = 0.26$). However, in the vertical dimension, 10 of 12 species showed significant differences in the number of visits. Only the Great Tit and the Chaffinch were observed equally often in all vertical strata. Four species favoured the upper crown including the Blue Tit, European Starling, Chiffchaff and the Lesser Spotted Woodpecker. The middle crown was mostly frequented by the Great Spotted Woodpecker, Pied Flycatcher, Nuthatch and the Short-toed Treecreeper. The Blackcap and the Middle Spotted Woodpecker foraged in the middle and in the lower crown (Fig. 4).

Analysing the horizontal stratification revealed that the Chaffinch used each horizontal stratum equally well without any significant differences. Four bird species preferred the outermost twigs of the tree-tops: the Chiffchaff, the Blackcap, the European Starling and the Blue Tit (Fig. 5). The Great Tit foraged frequently on the outermost branches as well, but it was also frequently observed in the central parts of the crowns. The microhabitat nearby, i.e. the stem inside the crown, was used by two species that are specialised foragers on bark: the Great Spotted Woodpecker

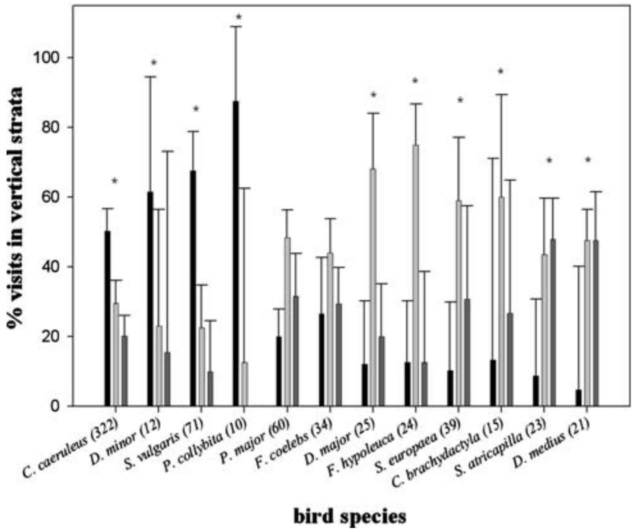

Fig. 4 Percentages of visits with standard deviation by 12 selected bird species in relation to vertical strata; *black* upper crown, *grey* middle crown; *dark grey* lower crown. Sample size is given in *parentheses*; *asterisk* significant difference (χ^2; all $P < 0.05$)

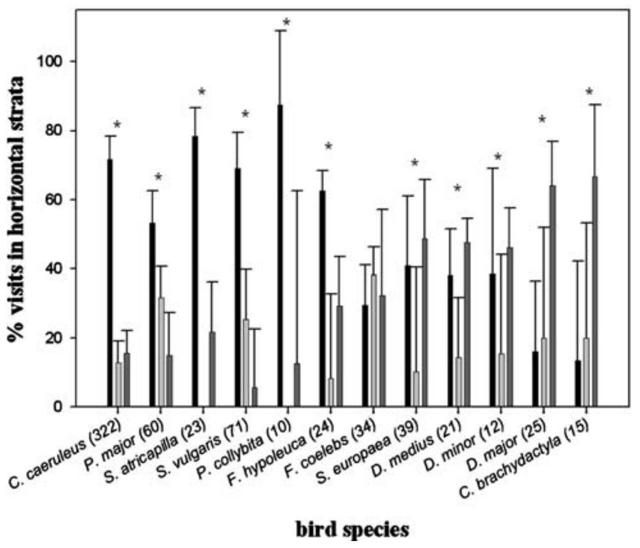

Fig. 5 Percentages of visits with regard to horizontal strata observed in the 12 selected bird species with standard deviation; *black* outermost branches; *grey* middle crown; *dark grey* inside of the crown. Sample size is given in *parentheses*; *asterisk* significant difference (χ^2; all $P < 0.05$)

and the Short-toed Treecreeper. We also observed Nuthatches, and the Middle as well as the Lesser Spotted Woodpecker, inside the crown as well as on the outermost branches but with fewer visits than near the trunk. The Pied Flycatcher foraged generally on the outermost branches and inside the crown (Fig. 5).

Foraging height

To illustrate possible differences in height preferences of the 12 bird species we calculated the foraging height index and identified three height categories (15–20, 21–25, 26–30 m). The Chiffchaff and the European Starling foraged mainly between 26 and 30 m above the forest floor and were looking for food significantly higher up in the vegetation than the Pied Flycatcher, Chaffinch, Nuthatch, Blackcap and Middle Spotted Woodpecker (all $P < 0.01$; Fig. 6). Eight species were observed somewhat lower, between 21 and 25 m above the forest floor (Lesser Spotted Woodpecker, Blue Tit, Short-toed Treecreeper, Great Spotted Woodpecker, Great Tit, Pied Flycatcher, Chaffinch, Nuthatch) while the Blackcap and the Middle Spotted Woodpecker foraged in lower crown layers between 15 and 20 m. As with the stratification, we did not find significant differences in the use of foraging height by the birds across the two tree species.

Foraging techniques

Comparing the foraging techniques performed by the 12 bird species revealed that each species preferably used one foraging strategy. Eleven of the 12 species favoured the foraging technique "gleaning" with more than 84%. Only the Pied Flycatcher preferred, as it is typical for this genus, the hovering technique (72.4%; Table 3).

Foraging substrate

The 12 species used several foraging substrates to various extents (Table 4). The lower surface of the leaf was preferred by most species over all other substrates. For example, Blue Tits, Great Tits, Blackcaps and Nuthatches gleaned prey mostly from the lower surface. The upper side of leaves as well as wood and air were used for foraging activities to a lesser extent. The Chaffinch foraged equally often on the upper side of leaves as well as

Fig. 6 Mean foraging height index of 12 selected bird species with standard deviation; *asterisk* significant difference (*U* test: $P \leq 0.01$)

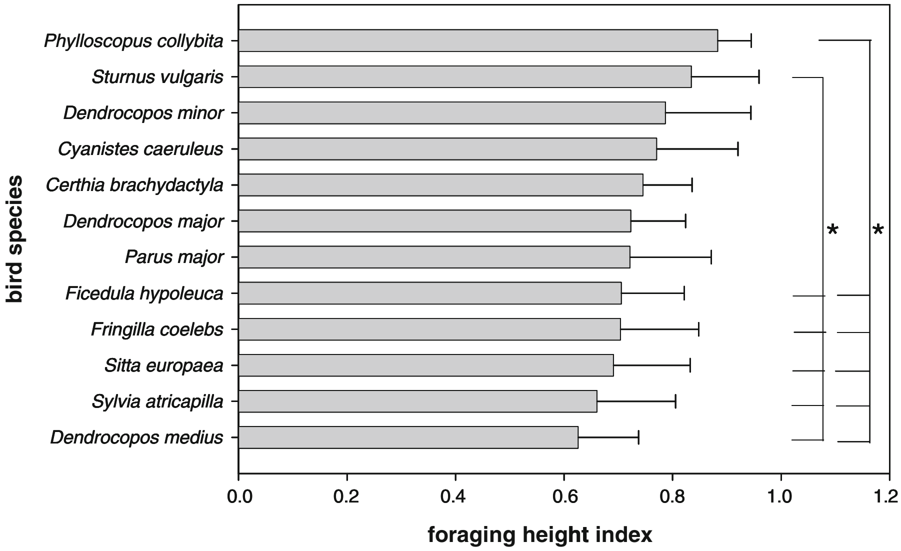

Table 3 Comparison of foraging techniques used by the 12 selected bird species given as % of total number of prey attacks

Bird species[a]	Glean	Jump	Probe	Hovering	Aerial	Statistics
Blue Tit (1,749)	97.9	0.1	1.8	0.2	0.1	$H = 136.37$; $P \leq 0.001$
Great Tit (284)	96.8	0.7	2.5	0.0	0.0	$H = 812.63$; $P \leq 0.001$
Chaffinch (107)	92.5	0.9	1.9	0.0	4.7	$H = 64.31$; $P \leq 0.001$
Great Spotted Woodpecker (39)	87.2	0.0	12.8	0.0	0.0	$H = 33.19$; $P \leq 0.001$
Middle Spotted Woodpecker (196)	96.9	0.0	3.1	0.0	0.0	$H = 57.76$; $P \leq 0.001$
Lesser Spotted Woodpecker (82)	84.1	0.0	15.9	0.0	0.0	$H = 37{,}987.00$; $P \leq 0.001$
Blackcap (96)	97.9	0.0	0.0	2.1	0.0	$H = 52.13$; $P \leq 0.001$
Pied Flycatcher (29)	24.1	0.0	3.4	72.4	0.0	$H = 45.02$; $P \leq 0.001$
Nuthatch (93)	94.6	0.0	3.2	2.2	0.0	$H = 115.15$; $P \leq 0.001$
European Starling (127)	96.9	0.0	3.1	0.0	0.0	$H = 94{,}981.00$; $P \leq 0.001$
Short-toed Treecreeper (36)	91.7	0.0	8.3	0.0	0.0	$H = 22{,}869.00$; $P \leq 0.001$
Chiffchaff (10)	100.0	0.0	0.0	0.0	0.0	$H = 28{,}603.00$; $P \leq 0.001$

[a] Sample size (number of observed prey attacks) is given in parentheses

Table 4 Comparison of feeding substrates used by the 12 selected bird species given as % of total number of prey attacks

Bird species[a]	Lower surface of leaf	Upper surface of leaf	Wood	Air	Statistics
Blue Tit (1,749)	56.3	8.4	35.1	0.2	$H = 142.30$; $P < 0.001$
Great Tit (284)	59.3	23.3	17.4	0	$H = 27.74$; $P < 0.001$
Chaffinch (107)	44.1	39	8.5	8.5	$H = 11.31$; $P = 0.010$
Great Spotted Woodpecker (39)	71.9	12.5	15.6	0	NS
Middle Spotted Woodpecker (196)	26.5	2.3	71.2	0	$H = 14.57$; $P = 0.002$
Lesser Spotted Woodpecker(82)	70.2	3.5	26.3	0	$H = 18.11$; $P < 0.001$
Blackcap (96)	73.5	8.8	17.6	0	$H = 11.58$; $P = 0.009$
Pied Flycatcher (29)	96.3	0	3.7	0	$H = 46.18$; $P < 0.001$
Nuthatch (93)	51.2	43.9	4.9	0	$H = 44.99$; $P < 0.001$
European Starling (127)	75.4	18	6.6	0	$H = 17.60$; $P < 0.001$
Short-toed Treecreeper (36)	57.1	14.3	28.6	0	NS
Chiffchaff (10)	66.7	33.3	0	0	$H = 9.37$; $P = 0.025$

NS Not significant

[a] Sample size (number of observed prey attacks) is given in parenthesis

on the lower leaf surface. Wood like other types of substrate as well as captures of flying insects in the air as a further food resource were used infrequently. The lower and the upper leaf surface were used by the European Starling much more in contrast to the other substrates. The Pied Flycatcher was highly specialised in contrast to the other species as it foraged almost exclusively (>90%) on the lower surface of the leaves. Substrate use by the woodpeckers and the Short-toed Treecreeper was opposite to the other bird species. The Great Spotted Woodpecker and the Short-toed Treecreeper used both sides of the leaves as well as wood in equal frequency. The Lesser Spotted Woodpecker showed a significant preference for the lower surface of leaves and wood and the Middle Spotted Woodpecker preferred wood as foraging substrate (Table 4).

Foraging and search rate

We calculated foraging and search rates of the bird species to assess possible differences in the use of common oaks and sycamore maples (Table 5) as well as throughout the observation period (Table 6). Only Great Tits revealed significant differences in foraging and search rate with regard to tree species. Both were significantly higher on sycamore maples than on common oaks (Table 5). Blue Tits also showed higher foraging rates on sycamore maples than on common oaks but their search rate was equal. The results of the European Starling were contradictory. Its foraging rate did not differ between the two tree species, but its search rate was significantly higher on common oaks than on sycamore maples (Table 5). The other bird species showed no significant differences in foraging and search

Table 5 Species-specific differences in foraging rate (=number of prey attacks/staying time) and search rate (=number of search movements/staying time) of seven selected bird species on sycamore maples and common oaks

Bird species[a]	Foraging rate		*U* test	*P*	Search rate		*t* test	*P*
	Common oak	Sycamore maple			Common oak	Sycamore maple		
Blue Tit (322)	0.08	0.12	9,903.00	$P < 0.001$	0.19	0.18	–	NS
Great Tit (60)	0.06	0.12	193.00	$P < 0.001$	0.15	0.21	2.26	0.031
European Starling (71)	0.09	0.07	–	NS	0.17	0.09	2.48	0.019
Middle Spotted Woodpecker (21)	0.08	0.06	–	NS	0.14	0.23	–	NS
Great Spotted Woodpecker (25)	0.07	0.07	–	NS	0.07	0.08	–	NS
Chaffinch (34)	0.06	0.08	–	NS	0.13	0.14	–	NS
Blackcap (23)	0.06	0.05	–	NS	0.16	0.19	–	NS

NS Not significant, – = low sample size

[a] Sample size is given in parentheses

Table 6 Seasonal differences in foraging (=number of prey attacks/staying time) and search rates (=number of search movements/staying time) of the 12 selected bird species

Bird species[a]	April		May	
	Foraging rate	Search rate	Foraging rate	Search rate
Blue Tit (322)	0.10	0.21	0.09	0.16
Great Tit (60)	0.12	0.22	0.04	0.13
Chaffinch (34)	0.07	0.11	0.06	0.14
Great Spotted Woodpecker (25)	0.10	0.08	0.06	0.07
Middle Spotted Woodpecker (21)	0.09	0.16	0.08	0.23
Lesser Spotted Woodpecker (12)	0.11	0.16	0.09	0.15
Blackcap (23)	0.05	0.15	0.06	0.14
Pied Flycatcher (24)	–	0.13	0.06	0.08
European Starling (71)	0.10	0.04	0.09	0.17
Nuthatch (39)	0.08	0.31	0.08	0.16
Short-toed Treecreepr (15)	–	–	0.07	0.24
Chiffchaff (10)	–	–	0.04	0.21

[a] Sample size is given in parentheses

rate between both tree species. Foraging and search rate of the remaining bird species, the Nuthatch, the Short-toed Treecreeper, the Lesser Spotted Woodpecker, the Chiffchaff and the Pied Flycatcher, could not be compared because sample size was too low for the sycamore maple.

Comparing the total values of the 12 bird species revealed significant differences in foraging rate ($H = 42.36$; $P \leq 0.001$) per staying time in either common oaks or sycamore maples. The Lesser Spotted Woodpecker performed the highest number of prey attacks with six attacks per staying time in addition to the two tits which also had similarly high foraging rates. These three species attacked prey more often per staying time than the Chiffchaff ($H = 14.12$; $P = 0.003$). The other species showed no significant differences in their foraging rate. The Pied Flycatcher and the Great Spotted Woodpecker had the lowest search rate per tree visit with on average 4.6 and 3.8 search movements per staying time.

Foraging and search rate differed during the study period in the Great Tit, Chiffchaff and Nuthatch. The foraging rate of Great Tits and Chiffchaffs decreased significantly during the observation period (Great Tit: $t = 4.40$; $P = 0.007$; Chiffchaff: $t = 2.88$; $P = 0.045$), whereas the search rates remained equal. The Nuthatch showed contrasting results. Its foraging rate did not vary during the observation period, but search rate dropped significantly ($t = 4.01$; $P = 0.01$) throughout the weeks. The other species showed no significant differences.

Searching behaviour

We classified the birds according to the distances at which each individual searched for and reacted towards prey during its staying time in a tree-top and discriminated between short-distance-searchers (≤50 cm) and long-distance-searchers (>50 cm). Overall, the bird species differed significantly in their use of search distances ($t = 206.00$; $P = 0.001$; Table 7). The Pied Flycatcher had on average the longest search distances among all species studied with more than 80% of its search moves. The other species showed mostly short distances (>65%).

Association of vegetation parameters with foraging behaviour of birds

As part of our study, we assessed the influence of vegetation parameters (see Appendix) on presence and activity of birds in individual trees. The results revealed that foraging behaviour of most bird species was influenced by tree characteristics.

Table 7 Average distance and short (≤50 cm) versus long distance (>50 cm) foraging given in % for the 12 selected bird species during prey search

Bird species[a]	Average ± SD (cm)	Distance ≤50 cm (%)	Distance >50 cm (%)
Pied Flycatcher (45)	110 ± 120	20	80
Nuthatch (264)	30 ± 40	80	20
Lesser Spotted Woodpecker (151)	30 ± 40	65	35
Blue Tit (2844)	30 ± 40	68	32
European Starling (235)	30 ± 75	78	22
Chiffchaff (56)	30 ± 30	75	25
Great Tit (385)	30 ± 40	73	27
Short-toed Treecreeper (112)	20 ± 30	88	12
Chaffinch (212)	30 ± 50	75	25
Blackcap (188)	20 ± 20	70	30
Middle Spotted Woodpecker (408)	20 ± 40	90	10
Great Spotted Woodpecker (50)	30 ± 40	80	20

[a] Sample size is given in parentheses

Multiple correlation analyses revealed that DBH and crown volume increased significantly ($r = 0.67$, $P < 0.001$) with increasing tree height. We compared tree size with the total number of bird visits (pooled data over the complete study period) and found that large trees were favoured by foraging birds ($r = 0.43$, $P < 0.001$). On the species-level, we detected different preferences of the selected bird species for tree characteristics (Table 8). Most bird species favoured tall trees with a large amount of dead wood. Furthermore, Blue Tits, Great Spotted Woodpeckers and Pied Flycatchers preferred tree individuals with a low crown density. However, Lesser Spotted Woodpecker, Blackcap and Short-toed Treecreeper did not show any preferences for one of the tree parameters.

Finally, we tested whether the spatial distribution of the birds differed between the western and eastern area of the crane plot. Interestingly, the western area, which is part of the nature reserve, was visited significantly more often than the eastern area ($t = 400.00$; $P = 0.035$) that is more disturbed by human activities. However, those differences were only significant for three species, the Blue Tit, the Great Tit and the Chaffinch, which occurred more often in the western part of the crane plot than in the eastern area.

Discussion

Our study focused on patterns of resource use of 12 selected bird species in the canopy of common oaks and sycamore maples throughout a 2-month period. Specifically, we concentrated on the preference of the birds regarding tree species and compared staying time and foraging technique in the tree crowns. We also documented stratification of birds in common oaks and sycamore maples and addressed the question whether and how tree preferences and foraging activity of the birds show seasonal changes with regard to tree phenology.

Preference of tree species

Our expectation that all birds should favour common oaks as main foraging area was confirmed for 9 of the 12 species. This is most likely linked to resource availability as the knotty bark of oak trees and the high percentage of dead wood provide substrate for a large variety and number of arthropods in contrast to the smooth and peeling bark of

Table 8 Association of 12 selected bird species with tree parameters

Bird species[a]	Tree size	Crown density	Dead wood	Overlap
Blue Tit (322)	$r = 0.89$; $P = 0.003$	$r = -0.87$; $P = 0.007$	$r = 0.99$; $P < 0.001$	NS
Great Tit (60)	$r = 0.64$; $P = 0.04$	NS	NS	NS
Chaffinch (34)	$r = 0.56$; $P = 0.03$	NS	$r = 0.99$; $P < 0.001$	NS
Great Spotted Woodpecker (25)	$r = 0.54$; $P = 0.02$	$r = -0.52$; $P = 0.03$	NS	NS
Middle Spotted Woodpecker (21)	$r = 0.56$; $P = 0.005$	NS	$r = 0.99$; $P < 0.001$	NS
Lesser Spotted Woodpecker (12)	NS	NS	NS	NS
Blackcap (23)	NS	NS	NS	NS
Pied Flycatcher (24)	$r = 0.56$; $P = 0.01$	$r = -0.60$; $P = 0.004$	NS	NS
European Starling (71)	$r = 0.76$; $P < 0.001$	NS	$r = 0.69$; $P = 0.008$	NS
Nuthatch (39)	$r = 0.61$; $P = 0.04$	NS	$r = 0.99$; $P < 0.001$	NS
Short-toed Treecreeper (15)	NS	NS	NS	NS
Chiffchaff (10)	$r = 0.68$; $P = 0.01$	NS	$r = 0,69$; $P < 0.001$	NS

NS not significant

[a] Sample size is given in parentheses

maple trees (Nicolai 1985; Lehmann 2004). As shown in a study of Utschick (2006) in southern Germany, insectivorous birds visit trees with higher food density more often and spend more time in their crowns while foraging activity is lower in trees with lower food supply.

Furthermore, species prefer those vegetation types which are better suited for their foraging techniques and where they are morphologically adapted for (Forstmeier and Keßler 2001). For instance, Pied Flycatchers are adapted to catch prey in short sally flights in the air or while hovering in front of substrate, i.e. leaves and branches. Such adaptations include long wings as well as a broad and flat bill with distinct bristles surrounding it, all of which facilitate capture of flying insects (Glutz von Blotzheim and Bauer 1993a). In this context, density of foliage and branches play important roles by permitting or constraining access to resources (Robinson and Holmes 1982). This is supported by our observations that Pied Flycatchers did not hunt in dense treetops most probably because they may have difficulties within dense vegetation in performing straight sally flights directed at food items detected over longer distances.

Contrary to our expectations and other studies (Glutz von Blotzheim and Bauer 1993a), Great Tits and Blackcaps did not show a clear preference for one of the two trees. As both species mainly feed on arthropods, the common oak should be preferred as it is likely to provide more food resources for insectivorous birds than the sycamore maple. Also, we did not find any preference for common oaks in the Middle Spotted Woodpecker. This was unexpected as well as this species is mostly known from oak forests (Glutz von Blotzheim and Bauer 1980). Overall, our results show that the Middle Spotted Woodpecker is not as specialised on oak trees over the whole year as proposed by other studies (e.g. Pettersson 1983). Probably, the high abundance of old sycamore maples in the study area, which possibly harbour a large number of arthropods, influenced our results of tree species preferences of these birds as they can detect prey easily and forage efficiently during the flowering time in both tree species. Our observations are also supported by a study of Pasinelli and Hegelbach (1997) who observed regular visits of maple trees by several individuals of the Middle Spotted Woodpecker and in part by Pettersson (1983) who states that the use of other tree species is most common in March and April, when leaf flush of ash and maple trees start.

Although most of the selected bird species showed generally a preference for oak trees, we assumed seasonal differences depending on leaf flush and flowering of the two tree species. As resource availability is likely to change in spring (Feeny 1970; Kraft and Denno 1982; Naef-Daenzer and Keller 1999; Murakami 2002), we asked whether and how changes in tree phenology are reflected in the birds' preferences for certain tree species (Smith and Dawkins 1971; Robinson and Holmes 1982; Gabbe et al. 2002). For example, caterpillars, which are high quality food to birds because of their substantial energy content (Feeny 1970), are most abundant in the canopy in the first weeks after the buds open (Murakami 2002). As birds are probably under high energy stress during this period, which covers migration as well as preparations for reproduction, they are likely to use habitats or specific microhabitats where they can cover more than their average daily energy budget at low costs (Moermond 1990). Consequently, we expected that the birds would first favour sycamore maples in April and then common oaks in May because of the different timing of leaf flush and flowering in both trees and hence different resource availability. Our hypothesis was supported for some species (Blue Tit, Great Tit, Chaffinch, Blackcap and European Starling) which changed their preference for tree species when leaf flush started in the common oak. Interestingly, all species that fed on the trunk (woodpeckers, Nuthatch and Short-toed Treecreeper) did not change tree preferences. Probably, those species do not depend on leaf flush and flowering as much as foliage gleaning birds because they spent their foraging time mostly on the bark (Glutz von Blotzheim and Bauer 1980, 1993b; Blume and Tiefenbach 1997).

Staying time

Assuming that staying time of birds in a tree crown mainly depends on resource availability and foraging strategy, we expected seasonal and species-specific differences. Both assumptions were supported. For instance, some bird species such as the Middle Spotted Woodpecker stayed on average much longer in a tree crown ($\sim$190 s) than the Pied Flycatcher which spent on average only 36 s in a tree top. In case of the Middle Spotted Woodpecker, some of the differences can be explained by differences in search strategy and probably also efficiency of foraging. The Middle Spotted Woodpecker is a "searching woodpecker" (Blume and Tiefenbach 1997). It mostly scans the substrate visually and rarely picks on the bark in contrast to the other co-existing woodpeckers, Great Spotted Woodpecker and Lesser Spotted Woodpecker, that use acoustic cues to detect food such as grubs by picking on the bark (Glutz von Blotzheim and Bauer 1980). The Lesser Spotted Woodpecker showed rather long staying times in comparison to other selected bird species (except the Middle Spotted Woodpecker). Probably, the Lesser Spotted Woodpecker had to glean large numbers of smaller arthropods (e.g. small Diptera, aphids) because of its smaller body size, and thus needed more searching movements and prey attacks per time window than the other woodpeckers which fed on larger prey items.

In contrast, the Pied Flycatcher foraged in short sally flights from a perch, visiting each tree only for a few seconds. This foraging technique must be very efficient, because our observations suggest that the Pied Flycatcher was successful in capturing prey in nearly all of the sally flights. Because of its late arrival in the breeding area, in the fourth observation week when availability of arthropods is likely to be much higher than in the first observation weeks, it encountered a rich variety of arthropods.

Vertical and horizontal stratification

Our data support our initial hypothesis that co-existing bird species may partition space by using species-specific spaces within tree crowns. Most birds favoured one or two of the crown strata, mostly the outermost twigs as well as the space next to the stem. Comparison of the two ecologically rather similar tits, Blue Tit and Great Tit, revealed distinct species-specific differences on the microhabitat scale. The larger Great Tit foraged more frequently in the middle of the crown and less on the outermost branches in contrast to the smaller Blue Tit. Perhaps body mass differences may account for this behaviour as the Great Tit is about twice as heavy as the Blue Tit (20 and 11 g, respectively; Glutz von Blotzheim and Bauer 1993a). Larger body mass might hinder efficient use of the outermost branches. Similar patterns have been observed by Alatalo and Moreno (1987) for the Willow Tit (*Parus montanus*) and the smaller Coal Tit (*Parus ater*). Those results suggest that birds are morphologically constrained in their capacity to forage optimally (Hutto 1990). Ultimately, those differences lead to differential use of tree strata and facilitate co-existence of different-sized, ecologically similar species.

Foraging techniques and foraging substrates

We expected differences in foraging behaviour of the selected bird species based on morphological adaptations. Furthermore, in addition to differential use of forest strata, choice of different substrates could also foster resource partitioning. We classified 11 of the 12 selected species as gleaning birds that take food directly from the substrate by sitting on trunks, twigs, petioles or leaves. Only the Pied Flycatcher exhibited the strategy of “aerial-gleaning” (72.4%), where the bird hovered in front of the vegetation and gleaned arthropods from leaves or branches. This contrasts with another study where up to 77% of the feeding attempts of the Pied Flycatcher were made by sally flights, only 14% by aerial-gleaning, 9% by landing on the ground and none by gleaning (Bibby and Green 1980). In our study, Pied Flycatchers did not make any sally flights and gleaning was used only infrequently (24%). The observed differences in foraging strategy might be linked to differences in type, availability and composition of prey. For instance, it is possible that the leaves offered more arthropods for the Pied Flycatcher in early spring, including various flightless larval stages. Hence, gleaning arthropods from leaves by hovering might be a more efficient foraging strategy in early spring, when only a low number of insects are available in mid-air.

We also compared the substrates used by foraging birds to detect possible differences between bird species and to relate them to tree species and phenology. Overall, the 12 species showed high flexibility in the use of foraging substrates. Interestingly, the European Starling preferably took food from the lower surface of the leaves, despite its higher body mass. This is probably due to the fact that the European Starling can stretch itself very well, which helps in reaching leaves at distances of several centimetres from the perch (Glutz von Blotzheim and Bauer 1993c). Greenberg and Gradwohl (1980) suggested that high mobility is a prerequisite to capture prey from the lower surface of leaves. Moreover, the choice of foraging substrate used also depends on tree and foliage architecture (Whelan 2001). For instance, the distance between twigs and leaves, i.e. the length of the petioles, affects accessibility of the leaf surfaces for foraging birds (Holmes and Robinson 1981).

Foraging and searching activities

We calculated foraging rates as well as search rates of the selected birds to detect possible differences between species and to relate them to tree species and phenology. In addition to changes in staying time of some bird species in the tree crowns of common oaks and sycamore maples during the vegetation period in spring, our data also revealed significant differences in foraging and search rates of three bird species, Blue Tit, Great Tit and European Starling. Those differences were related to tree species which most likely reflected differences in food availability. Food availability combined with species-specific foraging strategies, morphological adaptations and selective habitat use, i.e. stratification, are likely to profoundly influence efficiency of resource use within species assemblages. This, in turn, contributes to a fine-grained resource partitioning that promotes co-existence of a range of ecologically similar species, i.e. Blue and Great Tits and the woodpecker species.

Furthermore, our initial expectations regarding a decrease in foraging and search rate as a result of changes in prey availability during the study period were supported confirming the close relationship between bird foraging habit and resource distribution (Alatalo 1980; Holmes and Schultz 1988; Murakami 2002). Foraging activity decreased in some bird species, including the Great Tit and the Chiffchaff, and search rates dropped in species such as the

Nuthatch. Probably, because of the higher energy demand of the adult birds in the breeding season, foraging and search rates stayed constantly high in most species during the observation weeks. In all bird species, juveniles hatched during the time when larger arthropods became available. After this time, we could not discern if prey was captured for the birds' own needs or for their nestlings.

Association of vegetation parameters with foraging behaviour of birds

As another aspect of our study, we linked foraging behaviour of birds to characteristics of individual trees. Our data revealed that the near-natural western area of the crane plot received significantly more bird visits in the crowns of common oaks and sycamore maples than the eastern part. Most likely, this difference was caused by differences in vegetation parameters including tree size, percentage of dead wood and density of the tree crown, all affecting the birds' foraging behaviour. Several studies have shown that individual trees can have a large impact on habitat selection by breeding birds (Gabbe et al. 2002; Utschick 2006). In our study, trees with higher volumes received more visits by foraging insectivorous birds than the other, somewhat smaller trees. As proposed by Utschick (2006), voluminous and tall trees are attractive to birds as they offer a variety of habitats for a multitude of arthropods, which, in turn, are taken by foraging birds.

As foraging behaviour is also influenced by tree architecture (Whelan 2001), density of tree crowns is of importance because it affects movements of the birds through the habitat as well as detection and capture of prey (Robinson and Holmes 1982). Here, density was negatively correlated with the number of visits of foraging bird species. Tree individuals with a lower density of foliage and fewer branches had more visits than individuals with a dense crown structure. Lower crown density is likely to permit easier access for birds, probably allowing more searching movements than dense foliage.

Overall, our study underscores that mobile crane systems provide excellent opportunities to investigate behaviour of canopy living birds in great detail. However, as the forest area covered by a crane is limited, only a small number of trees can be observed. Hence, depending on the goal of a study, it is crucial to monitor breeding bird species by acoustic and visual territory mapping and compare the number of breeding individuals with the number of foraging birds (breeding species and feeding guests). In our study, the maximum number of individuals which we observed simultaneously in tree tops was much higher in most species than the number of breeding individuals that we documented by a territory mapping. Furthermore, a mobile crane allows detailed measurements of habitat parameters that either cannot be obtained from the ground at all or is very difficult to obtain, such as estimates of crown density and the amount of dead wood in the canopy.

Our study on the use of the canopy by birds represents a valuable tool for a better understanding of the structure and composition of bird assemblages, including important ecological processes such as niche partitioning and resource utilisation. In future studies, additional parameters, i.e. estimates of abundance and diversity of arthropods and larger sample sizes, i.e., more tree species to be considered as well to close the gap between resource use and resource availability.

Conclusion

Overall, our analyses demonstrate that the observed bird community shows a clear niche partitioning with regard to resource use, i.e. food and (micro-) habitats. On the one hand, adaptations on specific foraging techniques and substrates play an important role for resource partitioning. On the other hand, there are also characteristics like body mass which contribute to the decision which parts of the canopies can be used efficiently by a bird species. Furthermore, our results of tree species preferences, staying times as well as foraging and search rates of the birds, can be traced back to changes in food availability, which depends largely on type of tree and phenology. The switch from the sycamore maple to the common oak demonstrates that oak trees offers better foraging conditions and a better food supply than maple trees, except for 2–3 weeks right after the vegetation succession of the common oaks had started and the buds of common oak were still premature. In turn, we assume that the abundance of arthropods, for example caterpillars, is influenced by the foraging activity of birds in the tree crowns. This underlines the ecological function of insectivorous birds as important predators and hence potential regulators of leaf chewing, herbivorous insects and other arthropods (e.g. Murakami and Nakano 2000; Van Bael and Brawn 2005).

Finally, our study underscores the importance of structure-rich forest stands with tall deciduous trees and voluminous canopies for insectivorous birds and the relevance of such stands for forest management strategies in relation to conservation.

Zusammenfassung

Ressourcennutzung einer Vogelgemeinschaft in den Baumkronen eines temperaten Auwaldes

In dieser Studie analysierten und verglichen wir verschiedene Parameter der Ressourcennutzung von Vögeln, indem

wir ihr Nahrungssuchverhalten im Kronenraum eines temperaten Auwaldes mit Hilfe eines Baumkronen-Kranes beobachteten. Wir konzentrierten uns dabei auf zwölf Vogelarten, dokumentierten ihr Furagierverhalten und analysierten saisonale Unterschiede in ihrer Aktivität bei der Nahrungssuche in den Kronen zweier ausgewählter Baumarten, der Stieleiche (*Quercus robur*) und des Bergahorns (*Acer pseudoplatanus*) während der Vegetationsperiode im Frühling. Wir beobachteten mögliche Baumartenpräferenzen sowie die Nutzung vertikaler und horizontaler Baumstraten durch die Vögel. Zudem dokumentierten wir die bevorzugten Nahrungssuchstrategien der Vogelarten. Des Weiteren untersuchten wir vegetative Parameter, wie Baumhöhe und Stammdurchmesser, die die Ressourcenaufteilung von Vögeln beeinflussen können. Alle ausgewählten Vogelarten unterschieden sich deutlich in ihrem Furagierverhalten, einschließlich der Präferenz von Baumarten und -straten sowie in ihren Techniken des Nahrungserwerbs. Die meisten Vogelarten bevorzugten für ihre Nahrungssuche Stieleichen. Dies steht wahrscheinlich mit dem höheren Nahrungsangebot und dem reicheren Vorkommen an Nahrungssubstraten, vor allem der rauhen Rindenstruktur, in Verbindung. Diese bietet im Gegensatz zur glatten Rinde des Bergahorns mehr Mikrohabitate für Arthropoden. Eine höhere Arthropodendichte wiederum erleichtert den Vögeln das Aufspüren und Erjagen von Beute. Wir klassifizierten die ausgewählten Vogelarten nach ihrem Furagierverhalten in zwei funktionale Gruppen. Mit Ausnahme des Trauerschnäppers (*Ficedula hypoleuca*) legten alle beobachteten Arten während ihrer Nahrungssuchaktivitäten kurze Distanzen (≤50 cm) innerhalb der Baumkronen zurück und sammelten ihre Beute direkt vom Substrat ab (gleaning). Im Gegensatz dazu furagierte der Trauerschnäpper im Rüttelflug und suchte seine Beute über größere Distanzen (>50 cm). Wir zeigen in unserer Studie, dass der Zugang der Baumkronenschicht mit Hilfe mobiler Kransysteme exzellente Möglichkeiten bietet, das Nahrungssuchverhalten von Vögeln im Kronendach zu beobachten und im Detail zu analysieren. Die Ergebnisse unserer Studie legen nahe, dass die Ressourcennutzung von Vögeln von Art und Häufigkeit der Beuteorganismen ebenso stark abhängt wie von strukturellen Unterschieden von Baum- und Blattcharakteristika. Dies spielt zusammen mit morphologischen Merkmalen der Vögel eine bedeutende Rolle in der Wahl des Furagierhabitates und in der Nischenaufteilung co-existierender Arten.

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Appendix

See Table 9.

Table 9 Vegetation parameters of the sycamore maple (*Acer pseudoplatanus*: *A*) and the common oak (*Quercus robur*: *Q*) in the study plot with identification number of the tree individuals

Tree_ID	Tree height (m)	Crown volume (m^3)	DBH (cm)	Crown density (cm)	Dead wood (m^3)	Overlap (%)
A1_1	27.7	1,493.4	65.3	175	0.00	80
A1_2	28	78.1	30.2	143	0.02	90
A1_3	27.6	173.0	58.9	143	0.13	80
A1_4	24.9	433.0	52.5	205	0.49	83
A2_1	30	883.1	57.3	224	0.00	50
A2_2	22.5	217.8	23.9	173	0.00	30
A2_3	20.6	263.1	35.0	186	0.00	50
A2_4	28.2	953.5	57.3	168	0.14	70
A3_1	29.8	489.2	44.6	130	0.00	82
A3_2	31.9	728.8	54.1	150	0.06	95
A3_3	31.9	496.1	50.9	130	0.59	88
A3_4	30.4	261.9	44.6	133	0.59	87
A4_1	33	916.3	60.5	236	0.14	57
A4_2	28.8	826.8	50.9	106	0.21	58
A4_3	29.2	725.5	41.4	138	3.93	60
A5_1	31.3	967.1	65.3	252	0.20	50
A5_2	28.7	712.2	66.8	209	0.49	57
A5_3	27	314.0	28.6	103	2.36	65
A5_4	20.1	244.3	27.1	170	4.71	77
A6_1	26.5	564.9	48.0	120	0.00	90
A6_2	24.8	767.1	57.0	90	0.04	80
A6_3	27	385.7	21.0	143	0.02	90
A6_4	26	369.5	32.0	128	0.07	90
Q1_1	30.7	1,017.9	122.5	175	64.40	57
Q1_2	31.6	1,123.1	106.6	143	111.53	73
Q2_1	32	1,477.5	97.1	280	44.57	43
Q2_2	39.7	947.9	128.9	277	106.23	67
Q3_1	19.4	64.0	22.3	145	0.59	47
Q3_2	26.8	904.8	50.9	183	3.14	53
Q3_3	25.3	318.8	35.0	224	3.53	67
Q3_4	21.3	324.8	31.8	201	7.56	77
Q3_5	26.2	597.1	47.7	231	8.64	88
Q4_1	32.6	1.0	58.9	205	0.07	23
Q4_2	35.3	134.0	49.3	91	10.60	47
Q4_3	35.8	2,264.0	95.5	157	2,270.00	47

Table 9 continued

Tree_ID	Tree height (m)	Crown volume (m^3)	DBH (cm)	Crown density (cm)	Dead wood (m^3)	Overlap (%)
Q5_1	32.4	1,429.8	67.5	307	0.98	47
Q5_2	27.4	516.9	31.8	222	25.92	52
Q6_1	32.7	2226.1	146.4	223	70.69	58

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