

Foraging ecology of two bark foraging passerine birds in an old-growth temperate forest

Peter Adamík & Martin Korňan

Adamík, P., Dept. of Zoology, Palacký University, tř. Svobody 26, 771 46, Olomouc, Czech Republic; e-mail: adamik@prfnw.upol.cz

Korňan, M., Center for Ecological Studies, Ústredie 14, 013 62 Veľke Rovné, Slovakia

Received 9 October 2003, accepted 29 December 2003

This study deals with the foraging ecology of two bark foraging birds Nuthatch (*Sitta europaea*) and Eurasian Treecreeper (*Certhia familiaris*) in an old-growth temperate montane forest (Mala Fatra Mts., Western Carpathians, Slovakia). Tree species preferences and foraging behaviour were studied during four breeding periods. Both species showed similar annual dynamics in tree species preference; Beech (*Fagus sylvatica*) was avoided whereas Norway Spruce (*Picea abies*) and Sycamore (*Acer pseudoplatanus*) were preferred. Both bird species showed clear year-to-year variation in foraging patterns on Beech, but not for other tree species. In all three tree species the trunk itself and the larger branches were the most preferred foraging substrates. The Treecreeper over-utilized the trunks of Beech, Spruce and Fir (*Abies alba*) but no such differences between Treecreeper and Nuthatch were found for either Sycamore or snags. Overall, Nuthatch tends to be a broad-niched forager employing a greater variety of foraging techniques (mainly the glean and probe strategy) than Treecreeper (mostly glean and occasionally flutter chase). According to the results of this study, single-year studies might give an inaccurate picture of tree species preference by bark foraging bird species. Tree species composition may play an important role in habitat quality for both Nuthatch and Treecreeper and have implications for forest management.



1. Introduction

The abundance, distribution and availability of food resources are believed to be the principle factors influencing habitat suitability for birds (Cody 1974, Martin 1987) with several recent studies supporting this view (Strong & Sherry 2000, Johnson & Sherry 2001, Fayt 2003). There are inherent methodological difficulties associated with quantifying food resources, evaluating food availability and prey selection (e.g. Cooper & Whitmore 1990, Johnson 2000). Studying foraging behav-

our has become widely accepted in both management studies and applications (e.g. Steeger & Hitchcock 1998, Gabbe *et al.* 2002) as an alternative whereby differences in microhabitat use and foraging behaviour are thought to reflect differences in the use of the food resources themselves (MacArthur 1958).

Several studies have pointed to the strong foraging preferences of some bird species for particular tree species (Holmes & Robinson 1981, Parrish 1995, Gabbe *et al.* 2002, Adamík *et al.* 2003). Apart from the theoretical considerations of such

studies for both niche theory and the mechanisms of species co-existence, they highlight the conflict of interest between species-specific tree and/or habitat requirements and contemporary forestry management practices (Imbeau & Desrochers 2002). Because current forestry practices demand high timber production old stands, characterised by well-grown trees, and snags, an important food, roost and nest resource for bark foragers, are widely disappearing (Michal & Petriček 1998). Cavity nesting and bark foraging birds are among the most sensitive species to broad-scale changes in stand composition in both species and age (Dickson *et al.* 1983, Angelstam & Mikusiński 1994). Both Nuthatch and Treecreeper seem to be ideal species for studying the effect of these changes. Their higher densities and smaller territories in comparison to some, albeit more threatened woodpecker species, enable more effective data sampling which might allow them to be used as indicator species for the wider bark foraging community.

Recommending appropriate management practices for bark foragers and cavity nesters, two frequently overlapping groups, demands that temporal variability in bird habitat requirements be considered. An error common to studies dealing with bird foraging ecology is their neglect of inter-annual heterogeneity in their data sets. Pooling data across varying temporal scales is thought to obscure important patterns in avian ecology (Hejl & Verner 1990 and citations therein). Thus, investigating bird foraging ecology in intact old-growth stands to identify annual differences in habitat requirements may provide valuable information necessary for forestry management.

Silviculture has almost exclusively replaced European temperate forest. Surviving remnants are to be found in the Carpathians and in eastern Poland (Fuller 1995, Michal & Petriček 1998). In this paper we describe the foraging ecology of two bark foraging passerines: Nuthatch *Sitta europaea* and Eurasian Treecreeper *Certhia familiaris* in a mixed montane old-growth forest remnant during four consecutive breeding seasons. Our principle goals are to: (i) describe the foraging ecology and behaviour of these two species in near primeval conditions, (ii) characterise their specific foraging responses to particular tree species, (iii) determine their preferences for a given tree species, and (iv)

identify temporal variation in their tree preferences and behaviour. These species-specific responses are to be interpreted within a forestry management context, a focus which has yet to be applied to Central Europe. Additionally, this is the first study on resource use by these two species in the intact conditions of a European temperate forest patch.

2. Material and methods

2.1. Study site

This study was conducted in the Šrámková National Nature Reserve in the Malá Fatra Mountains of north western Slovakia (49° 11' N, 19° 06' E) where one of the last ancient woodlands of the former Czechoslovakia (Korpel' 1989) is protected. Forest covers 80% of Malá Fatra National Park (22,600 ha). As a consequence of Wallachian colonization during the 16th century the uppermost part of the mountains has been converted to alpine meadow.

Surrounded by an extensive woodland area, the 250 ha Šrámková nature reserve represents the climax stage (age of forest stand > 150 years) of a mixed beech-fir European temperate forest. The site lies at an altitude ranging from 950 to 1200 meters a.s.l. with an average annual temperature of 4–5 °C, and a July isotherm of 10–11 °C. Numerous micro-successional patches of different size (ranging up to ca 2 ha) and of differing dynamics cause considerable spatial heterogeneity with trees of uneven age structure.

The current tree species composition (expressed as the relative tree frequency) at the study site is comprised of Beech *Fagus sylvatica* (44.8%), Silver Fir *Abies alba* (20.3%), Norway Spruce *Picea abies* (4.8%), Sycamore *Acer pseudoplatanus* (4.3%), and an admixture of Elm *Ulmus montana* (2.9%) and Rowan *Sorbus aucuparia* (2.4%). The shrub layer consists mainly of Hazel *Corylus avellana* (5.9%), and saplings of the above mentioned tree species. The herb layer is dominated by ferns *Dryopteris spp.*, *Athyrium filix-femina*, currants *Ribes*, forbs *Rubus*, grasses *Calamagrostis*, *Luzula* and bilberries *Vaccinium myrtillus*. Standing dead trees (snags) comprise 14.6% of tree dominance in the forest interior.

2.2. Data collection

Vegetation characteristics (diameter at breast height, density and basal area of all trees with a diameter > 3 cm, Table 1) were measured in the core area of the Šrámková nature reserve in circular plots with a radius 11.3 m ($n = 24$) following the procedures of Noon (1981). The measurements were carried out between August and mid-September in 1998–1999. The plots were evenly spaced in a rectangular grid system of 50×50 m which was originally used for mapping breeding bird territories Korňan (in prep.).

Foraging behaviour was studied in the four consecutive breeding seasons between 1997–2000 from June until the second half of July. The data were collected during calm days with an emphasis on morning bird activity (06:00–11:00 CET). The sampling of individuals was mainly achieved by regularly walking through the nature reserve. During the time of data collection we systematically moved and stopped at a ca 5 minute intervals and carefully scanned both trunks and canopies to locate foraging birds. This reduced the likelihood that we would locate birds mainly either by vocal or conspicuous behaviour (Recher & Gebski 1990). Because birds were not colour-banded, the same individuals may have been recorded several times during the field season, but on the other hand, our move and stop approach and precise territory mapping allowed us to move to other individuals and to reduce possible pseudo-replication bias. If an individual foraging bird was observed we recorded its position and behaviour with a delay of several seconds or we waited until it flew to another tree in order to avoid recording conspicuous behaviour.

To study specific foraging patterns we recorded the following variables: tree species used, position on a given tree (vertical or horizontal movement) and substrate use (trunk, branch, twig < half of bird's body diameter, leaves, needles and others). The height, ranging from the point of landing to that of take-off was estimated by eye. Because the observations were made by two persons, the two observers practiced estimating heights together and thus standardized their estimation abilities. Irrespective of the number of foraging attacks only one observation per bird per tree was recorded for the purposes of analysing resource use

Table 1. Vegetation characteristics (mean + SE) of the study site (Šrámková nature reserve). Vegetation measurements derive from 24 circular plots with a radius = 11.3 m.

Tree species	Density n/ha	Basal area m ² /ha
Beech		
<i>Fagus sylvatica</i>	209.4 (42.4)	16.8 (3.2)
Fir		
<i>Abies alba</i>	94.7 (16.8)	9.1 (1.9)
Hazel		
<i>Coryllus avellana</i>	27.4 (17.1)	0.6 (0.6)
Norway spruce		
<i>Picea abies</i>	22.4 (7.0)	3.2 (1.0)
Sycamore		
<i>Acer pseudoplatanus</i>	19.9 (10.7)	3.2 (1.8)
Elm		
<i>Ulmus montana</i>	13.7 (6.1)	0.1 (0.1)
Rowan		
<i>Sorbus aucuparia</i>	11.2 (13.7)	0.2 (0.2)
Snags	68.6 (12.4)	8.5 (2.1)
All trees together	459.9 (61.4)	42.7 (4.5)

and subsequent statistical analyses. However, to identify foraging versatility we continued to observe individuals up to a maximum of 60 seconds on a given tree and recorded all types of foraging techniques at specific substrates (Morrison 1984, Recher & Gebski 1990). The following foraging strategies were recorded: glean (a manoeuvre in which a single standing, climbing or hopping bird caught the prey at the substrate surface), hover (mainly a wing-powered manoeuvre in which a hovering bird caught prey at the substrate surface), probe (a subsurface manoeuvre in which a bird either penetrated the substrate or inserted its bill into bark crevices), sally (an airspace manoeuvre in which a bird flew from a perch to attack flying prey, in the case of Treecreeper this was mainly the flutter-chase strategy [sensu Remsen & Robinson 1990]).

2.3. Data analysis

To analyse inter-annual variation in the length of foraging bouts we used one-way ANOVA. The differences in the initial and final foraging height on different tree species were examined by two-

tailed t-test. Because our data can be arranged as a multiway contingency table we decided to use stepwise log-linear analysis to find the best model to fit the data (Fienberg 1980). For Nuthatch we constructed a $3 \times 2 \times 2 \times 2$ contingency table characterising bird foraging behaviour according to tree species (Beech, Silver Fir, snag), foraging substrate (trunk, branch), position on a tree (horizontal or vertical), and foraging strategy (gleaning or probing). Because of Treecreeper's stereotypical behaviour the data were arranged as a $5 \times 2 \times 2$ contingency table to examine the effect of tree species (Beech, Silver Fir, snag, Norway Spruce and Sycamore), foraging substrate (trunk, branch) and position on a tree (horizontal or vertical). To set the preferences for a particular tree species we used the tree preference index (TPI) expressed as:

$$\text{eq. 1. TPI} = (O - E)/E,$$

where O = the number of foraging observations recorded for a given bird species on a given tree species and E = the number of expected foraging observations that would had been observed if the birds had selected trees at random. The E variable was calculated by multiplying the total number of foraging observations for a given bird species by the frequency of occurrence of a given tree species. Negative values mean avoidance, while positive values indicate preference for a given tree species (Peck 1989). Another selection index (known as forage ratio) proposed by Manly *et al.* (1993) held identical results for our data.

3. Results

The amount of time Nuthatch spent intensively foraging at a particular tree species varied significantly between years on Beech (ANOVA, $F_{3,53} = 3.54$, $P = 0.02$) but not on Fir ($F_{3,57} = 0.51$, $P = 0.68$), Spruce ($F_{3,18} = 0.53$, $P = 0.67$), Sycamore ($F_{2,11} = 0.57$, $P = 0.58$) or snags taken as a whole ($F_{3,44} = 2.45$, $P = 0.08$). Overall, Nuthatch foraged most frequently on Fir (Fig. 1a), Beech (Fig. 1b) and snags. Taking into account tree availability the most preferred trees were Spruce, Sycamore, snags and Fir in descending order (Table 2, Fig. 2). Foraging on Beech was avoided.

Stepwise log-linear analysis indicated that the

Table 2. Use (%), pooled data) of tree species and substrates by Nuthatch and Treecreeper in an old-growth beech-fir forest in Malá Fatra National Park, Western Carpathians, Slovakia. Tree dominance represents study site tree species composition (see Methods).

	Nuthatch ^a	Treecreeper ^a	Tree dominance
Tree use (%)			
Beech	28.1	21.6	44.8
Fir	30.0	36.8	20.2
Spruce	10.8	12.1	4.8
Sycamore	7.4	13.4	4.3
Snags	23.6	16.0	14.7
Substrate (%)			
Trunk	35.2	69.9	
Branch	27.9	18.2	
Twig	17.5	4.3	
Leaf	17.7	4.5	
Air	1.7	3.0	

^aSample sizes: Nuthatch = 218; Treecreeper = 254

best model for Nuthatch foraging behaviour included the substrate-by-position, tree species-by-position, and tree species-by-strategy interactions ($\chi^2_{13} = 19.84$, $P = 0.10$). When nuthatches were foraging on Beech they avoided the trunk and hunted mainly in the crown on the branches and leaves. Preying on Fir has a similar pattern, with most activities spent on gleaning twigs, branches and then trunks. Foraging behaviour on snags has a specific pattern with most of the foraging manoeuvres on trunks being gleans, but an unusually high number of encounters was recorded with the probe strategy occurring evenly between the trunk and branches.

Between different years the amount of time Treecreeper spent foraging on a particular tree species significantly differed for Beech (ANOVA, $F_{3,46} = 4.61$, $P < 0.01$), but not for snags ($F_{3,33} = 0.17$, $P = 0.92$), Fir ($F_{3,79} = 1.11$, $P = 0.35$), Spruce ($F_{3,24} = 0.05$, $P = 0.99$) or for Sycamore ($F_{3,27} = 0.15$, $P = 0.93$). The Treecreeper foraged most frequently on Fir and Beech (Table 2). Taking into account tree availability, the most preferred tree species for Treecreeper foraging were Sycamore, Spruce, Fir and snags, while foraging on Beech was avoided (Table 2, Fig. 2).

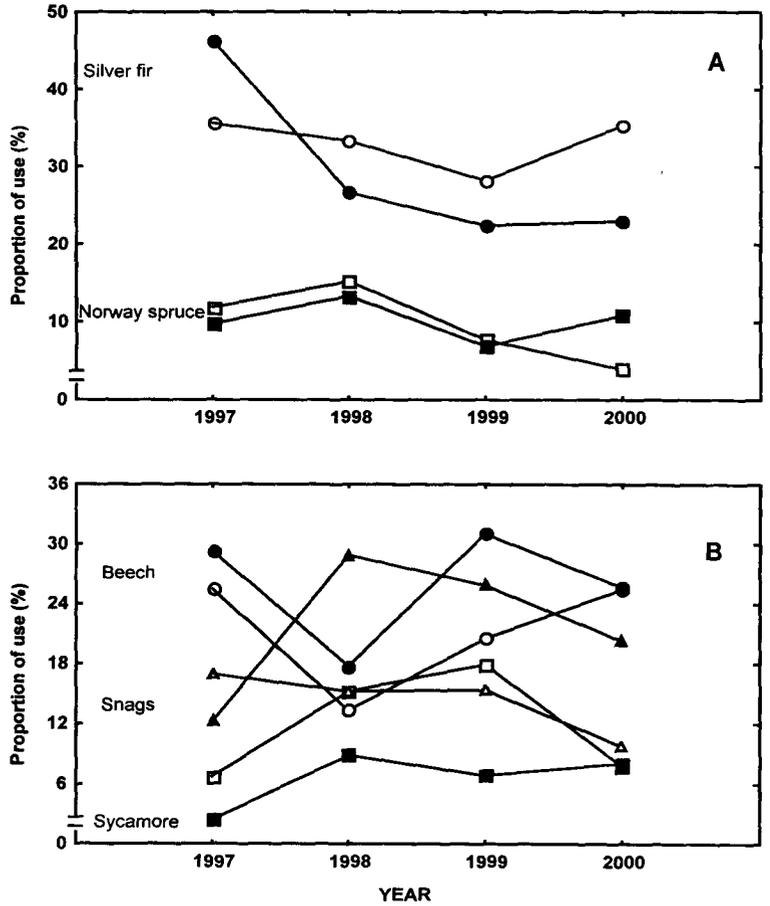


Fig. 1. Inter-annual changes in the use of coniferous trees (a), and deciduous trees and snags (b), as foraging substrates by Nuthatch (● ■ ▲) and Treecreeper (○ □ △) in an old-growth mixed forest.

Stepwise log-linear analysis indicated as a best model the substrate-by-position interaction and tree species main effect ($\chi^2_{12} = 19.78, P = 0.07$). The Treecreeper's behaviour is characterised by a stereotyped foraging pattern in which it mainly crept on trunks employing a vertical heads-up position using the glean strategy exclusively (Table 3). A similarly high proportion of vertical movement positions was maintained on branches.

When foraging on Beech the initial foraging height between Treecreeper and Nuthatch was significantly different ($t_{105} = 3.00, P < 0.01$, Table 4), but the final foraging height was not ($t_{105} = 0.28, P = 0.76$). The initial height on snags differed ($t_{83} = 2.34, P = 0.02$), but the final height did not ($t_{83} = 1.01, P = 0.31$). Neither the initial nor the final foraging height differed on Fir ($t_{144} = 1.55, P = 0.12$; $t_{144} = 1.10, p = 0.27$) or on Spruce ($t_{40} = 1.49, P = 0.14$; $t_{40} = -0.33, p = 0.74$). On Sycamore the initial

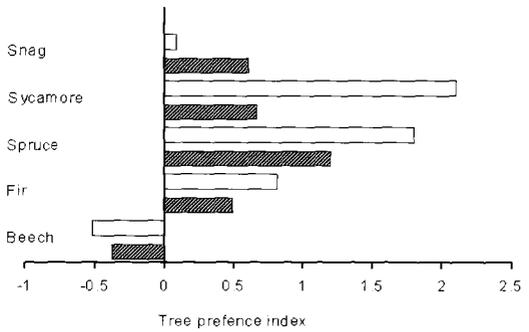


Fig. 2. Tree species preference index for Treecreeper *Certhia familiaris* (open bars) and Nuthatch *Sitta europaea* (hatched bars). The negative values indicate avoidance while positive values indicate preference for a given tree species.

foraging height did not significantly differ ($t_{44} = -0.67$, $P = 0.50$), but the final height did ($t_{44} = -2.07$, $P = 0.04$). With regard to the use of the trunk, the most common foraging substrate, there were tree-specific differences in use between Nuthatch and Treecreeper. Compared to Nuthatch, Treecreeper over-utilized the trunks of Beech (78% vs 22%, $\chi^2_1 = 18.18$, $P < 0.01$), Spruce (64% vs 20%, $\chi^2_1 = 8.49$, $P < 0.01$) and Fir (64% vs 19%, $\chi^2_1 = 25.23$, $P < 0.01$). However, there were no significant differences between Treecreeper and Nuthatch in the use of the trunk on either Sycamore (74% vs 64%, $\chi^2_1 = 0.14$, $P > 0.05$) or snags (89% vs 61%, $\chi^2_1 = 1.85$, $P > 0.05$), respectively.

4. Discussion

4.1. Foraging behaviour

Overall, Nuthatch employed a greater variety of foraging tactics and foraged more on substrates other than bark. The restricted use of both substrates and foraging techniques in Treecreeper results from its particular morphological adaptations to clinging on trunks (Norberg 1981, 1986). The Nuthatch is broad-niched and the Treecreeper narrow-niched at the generic level for both Europe and North America (Rabenold 1978, Morrison *et al.* 1987, Szekely 1987, Adams & Morrison 1993, Osiejuk 1996, Nour *et al.* 1997). The Treecreeper foraged on lower parts of the trunk which is a result consistent with the findings of other authors (Morrison *et al.* 1987, Weikel & Hayes 1999). This would seem to stem from two factors: the

Table 3. Proportional changes in use of foraging techniques^a of Nuthatch and Treecreeper in an old-growth beech-fir forest in Malá Fatra National Park during a four year period (1997–2000).

Year	1997	1998	1999	2000
Strategy				
Nuthatch				
Glean	81.5	81.4	68.7	83.0
Hover	12.3	5.7	2.4	0.0
Probe	6.2	11.4	25.3	15.1
Sally	0.0	1.4	3.6	1.9
Treecreeper				
Glean	98.5	90.7	92.3	97.0
Hover	0.0	5.0	0.0	0.0
Probe	0.0	0.0	3.9	0.8
Sally	1.5	4.3	3.9	2.3

^aSample sizes: Nuthatch = 65, 139, 52, 133; Treecreeper = 65, 70, 83, 159

bark on the lower part of the trunk is coarser and as a result may support higher densities of arthropods (Mariani & Manuwal 1990). In addition to which, as was previously mentioned, Treecreeper is limited to the trunk by its morphology while the Nuthatch is able to exploit a greater variety of substrates allowing it to readily switch from trunk to canopy when preying on insects found on leaves and needles.

4.2. Tree use

During the four-year period both species showed a similar pattern in the dynamics of tree species use.

Table 4. Initial (H_1) and final (H_2) mean heights (m, pooled data) of foraging bouts by Nuthatch *Sitta europaea* and Treecreeper *Certhia familiaris* in an old-growth montane forest.

	Foraging height			
	Nuthatch (n = 203)		Treecreeper (n = 231)	
	$H_1 \pm SD$	$H_2 \pm SD$	$H_1 \pm SD$	$H_2 \pm SD$
Beech	12.4 ± 6.7	13.0 ± 6.8	8.5 ± 6.7	12.6 ± 7.9
Fir	12.5 ± 6.4	14.4 ± 7.1	10.7 ± 7.6	15.9 ± 8.2
Snag	9.4 ± 5.4	12.9 ± 6.9	6.4 ± 6.4	11.2 ± 8.6
Spruce	13.5 ± 9.6	15.3 ± 9.1	8.4 ± 7.6	14.8 ± 8.8
Sycamore	7.2 ± 4.4	9.9 ± 4.9	8.2 ± 5.2	13.6 ± 6.1

Overall, Nuthatch displayed a greater use of Beech and snags while Treecreeper foraged more on Sycamore, Spruce and Fir. Taking into account tree availability, both species foraged on Beech less than would be expected. That is due to the smooth bark of the Beech which very probably supports less arthropod prey compared to tree species with fissured bark (Jackson 1979, Nicolai 1986, Mariani & Manuwal 1990). Beech is known to be poor in arthropod biomass (Kulfan 1990), and as Holmes and Robinson (1981) and Peck (1989) have found, beech is often avoided. The proposition that fissured bark plays an important role in avian foraging ecology can be supported by comparing the proportion of Nuthatch foraging on the trunk of different species. Of all the observations recorded on Sycamore and snags (both with highly fissured bark), 64% and 61% were recorded on the trunk, a finding in high contrast to trunk use on other tree species. The proposition would seem to be further supported by the initial foraging heights both of which were lower for Sycamore and snags than for other species. The similar annual dynamics in tree species use between these two bird species might be a consequence of opportunistic resource use as has been suggested from diet analyses (Kuitunen & Törmälä 1983, Kuitunen 1989, Krištín 1994).

However, the slight differences e.g. Treecreeper's higher preference for Sycamore and Nuthatch's higher preference for Beech could be better explained by the tree's structural characteristics. The Nuthatch, as a flexible forager, is able to compensate for the smooth bark of Beech by simply searching for prey on leaves. Here, the inadequacies of drawing conclusions from short-term studies in avian foraging and microhabitat selection hold true as is amply illustrated by our data from 1997 and 1998. Were we to have limited our study to just one of those two years we would have reached different conclusions about tree species preferences. For example, in 1997 Nuthatch foraged on snags in about 12% of cases while in the following year it was almost 29%. Similarly, in 1997 Treecreeper foraged on Sycamore in 7% of cases with use rising to about 15% the following year. Conclusions drawn from a one-year study might have revealed the same pattern, but importantly would have shown a different strength in tree preference. This supports our argument that

interpreting data collected on a short temporal scale risks being misleading.

In keeping with the results of Peck's (1989) study on tree species foraging preferences in six insectivorous birds, we find preferences by both species for Sycamore, but in contrast to her data, Treecreeper in our study showed significant preference for Norway Spruce. How might such an obvious difference be explained? The studies of Ulfstrand (1976, 1977) in Swedish conifer plantations indicate that Treecreeper foraged on Spruce at least in proportion to its availability. Geographic variation in species foraging behaviour may be an explanation. In Central Europe, Treecreeper inhabits primarily coniferous submontane and montane forests (Danko *et al.* 2002) so this difference might be due to the stand characteristic found at our study site. Because old-growth forests such as that of our study site are almost entirely gone comparing this result with structurally similar sites would be very difficult. We showed in an earlier study (Adamik *et al.* 2003) that habitat structure significantly affects the foraging niches of forest birds. When the bird foraging niches in a structurally heterogeneous old-growth forest were compared with those in a homogeneous spruce silviculture (Norway spruce 90% of tree dominance) all bird species had smaller niche breadth in the silviculture. In the spruce silviculture, where snags are rare, Treecreeper over-utilized snags as a foraging substrate (38% of foraging observations). Surprisingly, in Europe comparable data on the tree species preferences of these two bark foraging birds during the breeding season is lacking. Most published studies were conducted during the non-breeding season or in forests with very low tree species diversity (Nuthatch reviewed in Matthysen 1998). In deciduous forests Matthysen (1998) reports a general preference for oaks *Quercus* spp. over other tree species.

4.3. Link to forest management

Adams and Morrison (1993) have shown that Brown Creeper *Certhia americana* and Red-breasted Nuthatch *Sitta canadensis* prefer foraging on Incense Cedar *Calocedrus deccurens* which supports the highest arthropod densities on its coarse bark. However, as the authors point out,

this tree species is commercially non-attractive for foresters and is often removed. A similar conflict between bird habitat requirements and commercial interests is that of snags (Imbeau & Desrochers 2002). It is clear that in the absence of any of their preferred components birds will switch to other trees as a substitute resource base. Should these remaining bases not support food in sufficient quantities (or quality sites for nesting and roosting) then such habitat alteration leads to lower fitness and survival (Rolstad & Rolstad 2000, Suorsa *et al.* 2003). Aho *et al.* (1997, 1999) have found Treecreeper can be sensitive to ants whose presence on trunks can influence its foraging site selection and lower its fitness.

As this and other studies have found forest management should also take into consideration tree species composition (Holmes & Robinson 1981, Peck 1989, Gabbe *et al.* 2002). The Silver Fir is of special interest in forest management in Slovakia. Because of its past decline there has been an effort to increase its presence as a proportion of the Slovak forest base. Similarly, the high foraging preferences for Sycamore revealed in this study, demonstrate its important role in bird ecology. Beech is naturally the dominant tree species in temperate forest which suggests, yet based on our results beech forests may not be an ideal foraging habitat during the breeding season. However, this may reverse itself in autumn should there be a surplus of beech mast for Nuthatch (Nilsson 1987, Matthysen 1989). A more sustainable montane forest management strategy might consist of both an appropriate logging technique along with the restoration of certain key tree species.

Acknowledgements. R. T. Holmes, S. Sweeney, K. Weidinger, R. Virkkala and P. Fayt considerably improved earlier versions of the manuscript. Thanks also to E. Tkadlec for stimulating statistical discussions and to S. Bureš for methodological discussions. P. A. received support from the Ministry of Education of the Czech Republic (grant MSM 153100012 to the Laboratory of Ornithology, Palacký University).

Pähkinänakkelin ja puukiipijän ruokailuekologiasta lauhkean vyöhykkeen vanhoissa metsissä

Artikkelin kirjoittajat tutkivat päähkinänakkelin ja puukiipijän ruokailupuun valintaa ja ruokailu-

käyttäytymistä Slovakian aarniometsissä neljän pesimäkauden aikana vuosina 1997–2000.

Molemmat tutkimuslajit suosivat jokaisena tutkimusvuotena ruokailupuun valinnassaan kuusta ja vuorivaahteraa sekä välttivät pyökkiä. Vuosien välillä havaittiin sekä päähkinänakkelin että puukiipijän ruokailutavoissa vaihtelua pyökin suhteen, mutta ei muiden puulajien kohdalla. Puun runko ja suurimmat oksat olivat kaikkien puulajien kohdalla suosituimpia ruokailupaikkoja sekä päähkinänakkelilla että puukiipijällä. Puukiipijä hyödynsi oletettua enemmän pyökin, kuusen ja saksanpihdan runkoa. Vuorivaahteran tai kuolleiden puiden runkojen suosimista ruokailupaikkoina ei havaittu kummankaan tutkimuslajin kohdalla.

Tutkimustulosten mukaan päähkinänakkelin ruokailulokero on laajempi ja se käyttää useammanlaisia ruokailutekniikoita kuin puukiipijä. Kirjoittajat toteavat, että yhden vuoden tutkimusaineisto voi antaa vääristyneen kuvan puiden rungoilla ruokailevien lintulajien ruokailupaikan valinnasta tai ruokailutavoista. Kirjoittajat pohtivat lopuksi myös tulostensa merkitystä metsätalouden kannalta.

References

- Adamik, P., Korňan, M. & Vojtek, J. 2003: The effect of habitat structure on guild patterns and the foraging strategies of insectivorous birds in forests. — *Biologia* 58: 275–285.
- Adams, E. M. & Morrison, M. L. 1993: Effects of forest stand structure and composition on red-breasted nuthatches and brown creepers. — *J. Wildl. Manage.* 57: 616–629.
- Aho, T., Kuitunen, M., Suhonen, J., Jännti, A. & Hakkari, T. 1997: Behavioural responses of Eurasian treecreepers, *Certhia familiaris*, to competition with ants. — *Anim. Behav.* 54: 1283–1290.
- Aho, T., Kuitunen, M., Suhonen, J., Jännti, A. & Hakkari, T. 1999: Reproductive success of Eurasian Treecreepers, *Certhia familiaris*, lower in territories with wood ants. — *Ecology* 80: 998–1007.
- Angelstam, P. & Mikusiński, G. 1994: Woodpecker assemblages in natural and managed boreal and hemiboreal forest – a review. — *Ann. Zool. Fennici* 31: 157–172.
- Cody, M. L. 1974: Competition and structure of bird communities. — Princeton University Press, Princeton, NJ. 318 pp.

- Cooper, R. J. & Whitmore, R. C. 1990: Arthropod sampling methods in ornithology. — *Studies in Avian Biology* 13: 29–37.
- Danko, S., Darolová, A. & Krištín, A. (eds.) 2002: Birds distribution in Slovakia. — Veda, Bratislava, Slovakia. 688 pp. (In Slovak with English summaries.)
- Dickson, J. G., Conner, R. N. & Williamson, J. H. 1983: Snag retention increases bird use of a clear-cut. — *J. Wildl. Manage.* 47: 799–804.
- Fayt, P. 2003: Insect prey population changes in habitats with declining vs. stable Three-toed Woodpecker *Picoides tridactylus* populations. — *Ornis Fenn.* 80: 182–192.
- Fienberg, S. E. 1980: The analysis of cross-classified categorical data. — MIT Press, Cambridge, MA. 198 pp.
- Fuller, R. 1995: Bird life of woodland and forest. — Cambridge University Press, Cambridge, UK. 244 pp.
- Gabbe, A. P., Robinson, S. K. & Brawn, J. D. 2002: Tree species preferences of foraging insectivorous birds: implications for floodplain forest restoration. — *Cons. Biol.* 16: 462–470.
- Hejl, S. J. & Verner, J. 1990: Within-season and yearly variations in avian foraging locations. — *Studies in Avian Biology* 13: 202–209.
- Holmes, R. T. & Robinson, S. K. 1981: Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. — *Oecol.* 48: 31–35.
- Imbeau, L. & Desrochers, A. 2002: Foraging ecology and use of drumming trees by the three-toed woodpeckers. — *J. Wildl. Manage.* 66: 222–231.
- Jackson, J. A. 1979: Tree surfaces as a foraging substrates for insectivorous birds. — In: Dickson, J. G., Conner, R. N., Fleet, R. R., Kroll, J. C. & Jackson, J. A. (eds.), *The role of insectivorous birds in forest ecosystems*: 69–93. Academic Press, London, UK. 381 pp.
- Johnson, M. D. 2000: Evaluation of an arthropod sampling technique for measuring food availability for forest insectivorous birds. — *J. Field Ornithol.* 71: 88–109.
- Johnson, M. D. & Sherry, T. W. 2001: Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. — *J. Anim. Ecol.* 70: 546–560.
- Korpeľ, Š. 1989: *Pralesy Slovenska* [Primeval forests of Slovakia.] — Veda, Bratislava, Czechoslovakia. 332 pp. (In Slovak.)
- Krištín, A. 1994: Food variability of Nuthatch nestlings (*Sitta europaea*) in mixed beech forest: where are limits of its polyphagy? — *Biologia* 49: 773–779.
- Kuitunen, M. 1989: Food supply and reproduction in the Common Treecreeper (*Certhia familiaris*). — *Ann. Zool. Fennici* 26: 25–33.
- Kuitunen, M. & Törmälä, T. 1983: The food of Treecreeper *Certhia f. familiaris* nestlings in southern Finland. — *Ornis Fenn.* 60:42–44.
- Kulfan, M. 1990: Communities of butterfly caterpillars (Lepidoptera) on leaf timber species in Little Carpathians. — Veda, Bratislava, Czechoslovakia. 142 pp. (In Slovak with English summary.)
- MacArthur, R. H. 1958: Population ecology of some warblers of northeastern coniferous forest. — *Ecology* 39: 599–619.
- Manly, B. F. J., McDonald, L. L., & Thomas, D. L. 1993: Resource selection by animals: Statistical design and analysis for field studies. — Chapman and Hall, London. 175 pp.
- Mariani, J. M. & Manuwal, D. A. 1990: Factors influencing Brown Creeper (*Certhia americana*) abundance patterns in the southern Washington Cascade Range. — *Studies in Avian Biology* 13: 53–57.
- Martin, T. E. 1987: Food as a limit on breeding birds: a life history perspective. — *Ann. Rev. Ecol. Syst.* 18: 453–487.
- Matthysen, E. 1989: Nuthatch *Sitta europaea* demography, beech mast, and territoriality. — *Ornis Scand.* 20: 278–282.
- Matthysen, E. 1998: *The Nuthatches*. — Academic Press, London, UK. 315 pp.
- Michal, I. & Petříček, V. (eds.) 1998: *Péče o chráněná území. Lesní společenstva*. [Management of protected areas. Vol. 2: Forest communities.] — AOPK, Prague, Czech Republic. 714 pp. (In Czech.)
- Morrison, M. L. 1984: Influence of sample size and sampling design on analysis of avian foraging behavior. — *Condor* 86: 146–150.
- Morrison, M. L., With, K. A., Timossi, I. C., Block, W. M. & Milne, K. A. 1987: Foraging behaviour of bark-foraging birds in the Sierra Nevada. — *Condor* 89: 201–204.
- Nicolai, V. 1986: The bark of trees: thermal properties, microclimate and fauna. — *Oecol.* 69: 148–160.
- Nilsson, S. G. 1987: Limitation and regulation of population density in the Nuthatch *Sitta europaea* (*Aves*) breeding in natural cavities. — *J. Anim. Ecol.* 56: 921–937.
- Noon, B. R. 1981: Techniques for mapping avian habitats. — In: Capen, D. E. (ed.), *The use of multivariate statistics in studies of wildlife habitat*: 42–49. USDA Forest Service General Technical Report RM-87, Fort Collins, CO. 244 pp.
- Norberg, R. A. 1981: Why birds in trees should climb and hop upwards rather than downwards. — *Ibis* 123: 281–288.
- Norberg, R. A. 1986: Treecreeper climbing, mechanics, energetics, and structural adaptations. — *Ornis Scand.* 17: 191–209.
- Nour, N., Suhonen, J., van Damme, R., Matthysen, E. & Dhondt, A. A. 1997: Does the dominant Nuthatch *Sitta europaea* affect foraging behaviour of the subordinate Treecreeper *Certhia brachydactyla* in small forest fragments? — *Ardea* 85: 259–268.
- Osiejuk, T. S. 1996: Locomotion patterns in winter bark-foraging birds. — *Ornis Fenn.* 73: 157–167.
- Parrish, J. D. 1995: Effects of needle architecture on warbler habitat selection in a coastal spruce forest. — *Ecology* 76: 1813–1820.
- Peck, K. M. 1989: Tree species preferences shown by for-

- aging birds in forest plantations in Northern England. — *Biol. Conserv.* 48: 41–57.
- Rabenold, K. N. 1978: Foraging strategies, diversity, and seasonality in bird communities of Appalachian spruce-fir forest. — *Ecol. Monogr.* 48: 397–424.
- Remsen, J. V. & Robinson, S. K. 1990: A classification scheme for foraging behavior of birds in terrestrial habitats. — *Studies in Avian Biology* 13: 133–160.
- Recher, H. F. & Gebski, V. 1990: Analysis of the foraging ecology of eucalypt forest birds: Sequential versus single-point observations. — *Studies in Avian Biology* 13: 174–180.
- Rolstad, J. & Rolstad E. 2000: Influence of large snow depths on Black Woodpecker *Dryocopus martius* foraging behaviour. — *Ornis Fenn.* 77: 65–70.
- Steeger, C. & Hitchcock, C. L. 1998: Influence of forest structure and diseases on nest-site selection by red-breasted nuthatches. — *J. Wildl. Manage.* 62: 1394–1358.
- Strong, A. M. & Sherry, T. W. 2000: Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. — *J. Anim. Ecol.* 69: 883–895.
- Suorsa, P., Huhta, E., Nikula, A., Nikinmaa, M., Jäntti, A., Helle, H. & Hakkarainen, H. 2003: Forest management is associated with physiological stress in an old-growth forest passerine. — *Proc. R. Soc. Lond. B* 270: 963–969.
- Szekely, T. 1987: Foraging behaviour of woodpeckers (*Dendrocopos* spp.), Nuthatch (*Sitta europaea*) and Treecreeper (*Certhia* sp.) in winter and spring. — *Ekol. Pol.* 35: 101–114.
- Ulfstrand, S. 1976: Feeding niches of some passerine birds in a South Swedish coniferous plantation in winter and summer. — *Ornis Scand.* 7: 21–27.
- Ulfstrand, S. 1977: Foraging niche dynamics and overlap in a guild of passerine birds in a South Swedish coniferous woodland. — *Oecol.* 27: 23–45.
- Weikel, J. M. & Hayes, J. P. 1999: The foraging ecology of cavity-nesting birds in young forests of the northern coast range of Oregon. — *Condor* 101: 58–66.