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Locomotion patterns in wintering bark-foraging birds

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Locomotion patterns in the bark-foraging guild, three woodpeckers (*Dendrocopos major, D. medius, D. minor*) and three passerines (*Sitta europaea, Certhia brachydactyla* and *C. familiaris*), were studied during five winters (1990–1995) in mixed forests in Western Poland. The main aim of the study was to find the differences in locomotion between the studied species, as they might be important as a factor reducing competition for limited and unrenewable winter food resources. Locomotion and microhabitat utilization variables were used to obtain, on the basis of PCA, a smaller number of compound components describing mobility in foraging behaviour. PCA was also used to obtain a species body-size measurement from several external measurements. Interspecific differentiation of locomotion variables was very high and significant. Mobility of species was inversely correlated to body-size which was expressed specially in length of movement, speed of creeping, and ratio of foraging with stationary and dynamic patterns. Mean time of foraging on a tree was significantly longer in larger species, which was connected with the use of deep-foraging techniques by these species. Considering locomotion patterns, woodpeckers and passerines did not form strongly separate groups. Only both treecreepers showed very similar moving strategies, however, in this case also some significant differences were found.

1. Introduction

After the niche concept became important in understanding the structure of bird communities, many studies concerning the foraging behaviour of the bark-foraging guild were conducted. These studies mainly focused on the multidimensional niche partitioning (Selander & Giller 1959, Szekely 1987, Vanicsek 1988, Török 1990, Osiejuk 1992), seasonal changes (Conner 1981) or sexual dimorphism in foraging behaviour (Hogstad 1971, 1976, 1991, Peters & Grubb 1983, Aulén & Lundberg 1991, Suhonen & Kuitunen 1991, Matthysen et al. 1991, Osiejuk 1994). In addition, the methods of observation were almost always concentrated on describing the places of foraging (microhabitats) and on feeding techniques. Such investigations could give a lot of information about niche utilization, providing a little insight into locomotion patterns. Although members of the bark-foraging guild utilize the same microhabitats with similar techniques, they arrive at these places in different ways. For example, some species prefer to move along trunks or branches, while others reach their foraging microhabitats mainly by flying. Therefore, energy costs and risks of predation vary when different locomotion patterns are applied (Krebs & Davies 1987). These differences in locomotion between bark-foraging species may also make coexistence between them possible, because it reduces direct competition for limited and unrenewable winter food resources (Milinski & Parker 1991).

In this paper, I investigated the locomotion patterns of three European woodpeckers from genus *Dendrocopos*, the Eurasian Nuthatch *Sitta europaea* and two treecreepers *Certhia* spp. in sympatry. I assumed that different morphologies will exhibit different (1) energy costs of locomotion, (2) risk of predation, and (3) foraging behaviour, as a main determining factor of appliable feeding techniques and microhabitat utilization. The most important questions addressed are:

1. Are there any relations between locomotion patterns, foraging behaviour and body-size at the guild level?
2. Do woodpeckers and passerines form separate groups in terms of locomotion patterns?
3. Are the two treecreeper species similar in their locomotion patterns or not?

The detailed study on foraging niche utilization, based on the same material, is the subject of a different paper.

2. Materials and methods

The study was conducted during the five winters between 1990 and 1995 in a mixed forest near Poznań (Wielkopolski National Park — 52°15´N, 16°50´E) on an area of about 2 km^2. The dominant tree species are Scotch pine *Pinus sylvestris* and oak *Quercus robur*, mixed with the less numerous hornbeam *Carpinus betulus*, birches *Betula* spp. and maples *Acer* spp. (for more detailed descriptions, see Osiejuk 1993, 1994).

The foraging behaviour of birds was observed between 8:00 and 12:00, from 1 December to 28 February during each winter. To minimize the effects of weather on foraging behaviour, observations were made only on fine days.

The one-tree-one-record observation method was used (1T1R, Matsuoka 1977, Ishida 1990). The basic unit of analysed data was a set of observations collected from a tree, with the timing of several variables (see list following). As a consequence of the 1T1R method used, the observations might contain more than one category for some variables. For example, an individual might forage for 60 seconds on an oak and use two foraging techniques: gleaning for 20 seconds and probing for 40 seconds, and spends maybe 30 seconds on the trunk and 30 seconds on branches ∅ 20 cm, etc.

Observations, which were taken during a random walk in the study area, were not started when the birds were sighted but after their first flight among the trees. A maximum of five observations were made per individual before another bird was located (see Wiens et al. 1970, Short 1971, Peters & Grubb 1983). Birds were observed with 10 × 50 power binoculars. Foraging variables were noted using a dictaphone which was turned on throughout the whole observation. Subsequently, variables connected with time were measured with the aid of a stopwatch. Data for five years were pooled.

The following variables are analysed in this paper:

Locomotion variables:

a) Time of foraging on a tree (sec) — TF,
b) Ratio of foraging with dynamic and stationary pattern (obtained for each species as a quotient of total time foraging in a stationary pattern and total time foraging in a dynamic pattern; stationary pattern was understood to be foraging in one place on a tree without any movements and dynamic pattern was foraging while constantly moving along trunk or branches) — DS ratio,
c) Initial height of movement (m) — H_1,
d) Final height of movement (m) — H_2,
e) Length of movements (m) — $LM = (H_1 - H_2)$ (with due regard for movements along horizontal branches),
f) Speed of movements (m/minute) — $SPEED = LM/(TF/60)$,
g) Length of flights between trees (m) — LF.

Microhabitat utilization variables:

a) Tree species (Scotch Pine, Oak, other deciduous) — TREESPE,
b) Tree condition (dead or alive) — TRECON,
c) Foraging place (trunk, large branches — ∅ > 10 cm, medium branches ∅ 5–10 cm, small branches ∅ < 5 cm) — FORPLA,
d) Foraging technique (gleaning — picking invertebrates from the surface; probing — peering and poking for arthropods on the surface; scaling — scaling the bark of dead branches

or trunks for food; excavating — subcambial excavation; picking up cones and husking, earth gleaning — picking invertebrates from the surface of the ground) — FORTEC.

To analyse relations between locomotion and body-size I used the total body-size measurement (later size), which was obtained from principal component analysis of several log-transformed external measurements (see Freeman & Jackson 1990, Piersma & Davidson 1991) (Table 1). The measurements of birds were taken by the author from living birds nesting in Poland but not always from those breeding in the study area. All morphometric variables had positive loadings on the first component and similar magnitude (0.72–0.99).

The resident bark-foraging guild consisted of tree woodpecker species: Great Spotted Woodpecker *Dendrocopos major*, Middle Spotted Woodpecker *D. medius* and Lesser Spotted Woodpecker *D. minor*, Eurasian Nuthatch *Sitta europaea*, Short-toed Treecreeper *Certhia brachydactyla* and Eurasian Treecreeper *C. familiaris*. Black Woodpecker *Dryocopus martius* was also observed but it was excluded from the analysis due to insufficient data collected. Numbers and total times of observations for each species are given in Table 2.

Locomotion and microhabitat utilization variables are not independent of each other. Therefore, principal component analysis, using a correlation matrix of log-transformed data, was performed to obtain a few independent compound variables describing foraging behaviour in a simpler way.

3. Results

3.1. Interspecific differentiation of locomotion patterns

All interspecific differences in locomotion variables were statistically significant (Table 2). Mean TF was rather similar in all species except *D. major*, which had a mean TF about two times longer. The minimum observation time was similar in all species (5–8 sec). The longest observation was found in *D. major* (12 minutes of continuous feeding on a tree).

Both treecreepers used almost exclusively a dynamic foraging pattern (95–97% of feeding time), while *S. europaea* and *D. medius* spent 30–40% of the feeding time using the stationary pattern. *D. major* and *D. minor* were quite similar

Table 1. Total body-size index derived as first component from principal component analysis with varimax rotation.

Variable	Loading on PC1 = size
Flattened wing chord	0.97
Tail length	0.79
Bill length	0.99
Tarsus length	0.88
Body Mass	0.98
Eigenvalue	4.29
% variance explained	85.9

Table 2. Number of observations, total time of observations and locomotion variables of six studied species. ANOVA test performed for log transformed data. Size = total body-size measure obtained from PCA of several external measurements, DS = ratio of foraging with dynamic and stationary pattern, TF = mean time of foraging on tree (sec), H_1 = mean initial height of movement (m), H_2 = mean final height of movement (m), LM = mean length of movements (m), SPEED = mean speed of movements (m/min), LF = mean length of flights (m), *D. maj* = Great Spotted Woodpecker, *D. med* = Middle Spotted Woodpecker, *D. min* = Lesser Spotted Woodpecker, *S. eur* = Eurasian Nuthatch, *C. bra* = Short-toed Treecreeper, *C. fam* = Eurasian Treecreeper.

Species	N	Time (h:min)	Size	DS	TF ± SD	H_1 ± SD	H_2 ± SD	LM ± SD	SPEED ± SD	LF ± SD
D. maj	797	29:23	1.498	0.19	134 ± 134	15.4 ± 5.4	15.7 ± 5.3	0.3 ± 0.7	0.2 ± 0.9	15 ± 15
D. med	288	6:27	0.934	1.53	81 ± 82	13.4 ± 4.0	13.8 ± 4.1	0.5 ± 0.7	1.4 ± 2.8	8 ± 20
D. min	637	2:10	– 0.359	0.35	56 ± 46	13.0 ± 5.8	14.0 ± 5.0	1.0 ± 1.7	2.3 ± 3.8	15 ± 9
S. eur	560	13:06	– 0.230	2.34	75 ± 96	7.6 ± 4.3	8.4 ± 4.5	1.0 ± 1.6	0.9 ± 1.4	3 ± 7
C. bra	560	11:35	– 0.894	20.58	74 ± 98	6.6 ± 5.2	10.0 ± 5.0	3.4 ± 3.6	2.9 ± 2.2	5 ± 8
C. fam	420	7:47	– 0.949	31.83	67 ± 70	6.8 ± 4.7	10.1 ± 4.7	3.3 ± 3.3	3.6 ± 3.5	7 ± 8
ANOVA F					26.776	192.483	109.053	266.036	297.579	185.594
P-level					< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

and foraged in the stationary pattern more than other species (84.2% and 74.1%, respectively).

Considering the length of movements, both *Certhia* species were notably different from woodpeckers and the Nuthatch because they had the longest mean LM (Table 2). The difference between the treecreepers mean LM was insignificant (Newman-Keuls test, P = 0.829).

Taking into consideration H_1 and H_2 values, the passerines and woodpeckers formed separate groups (Table 2). The differences between most similar species, i.e. *C. brachydactyla* and *C. familiaris*, were significant only in the case of H_1 (Newman-Keuls test, P = 0.004 and P = 0.138, for H_1 and H_2 respectively). The fastest species were *C. familiaris* and *C. brachydactyla*, and the slowest species was *D. major* (Table 2).

The difference between mean creeping speed of treecreepers was significant (Newman-Keuls test, P = 0.012). The mean distance of flights between places of foraging in the studied species varied between 8 and 15 metres (Table 2). The shortest mean flight distances were found in *S. europaea*, the longest one in *D. minor* and in *D. major*. The differences between treecreepers was significant (Newman-Keuls test, P < 0.001).

From information on the time of foraging, the mean flight frequency was derived (flight frequency = mean TF/3 600 sec (flights per hour)). *D. major* flew, on an average, only 27 times per hour, *S. europaea*, *D. medius*, and *C. brachydactyla* 1.7–1.75 times more, and *C. familiaris* and *D. minor* 2–2.37 times more.

Although the treecreepers' locomotion patterns were very similar, some differences were found. *C. brachydactyla* foraged longer on oaks and on other deciduous trees, while *C. familiaris* foraged longer on pines (Newman-Keuls test, P = 0.889, P < 0.0001 and P < 0.0001, respectively). *C. brachydactyla* foraged longer on living trees, while *C. familiaris* foraged longer on dead ones (Newman-Keuls test, P = 0.879, P = 0.030, respectively). *C. brachydactyla* had a longer mean LM on oaks and living trees (Newman-Keuls test, P = 0.065 and P = 0.482, respectively) while *C. familiaris* crept, on average, longer on pines and dead trees (Newman-Keuls test, P < 0.001, P = 0.069, respectively).

Some microhabitat utilization variables appeared not to be directly related to specific locomotion variables (for example, TRECON, FORPLA) when examined for the whole guild.

Table 3. Percentage of foraging time in different microhabitats and with different techniques.

Variable		*Dendrocopos*		*Sitta*	*Certhia*	
	major	*medius*	*minor*	*europaea*	*brachydactyla*	*familiaris*
Tree species						
Scotch Pine	73.1	19.9	9.5	33.2	16.5	47.6
Oak	19.9	69.8	62.0	43.5	53.3	37.3
Other deciduous	7.0	10.3	28.5	23.3	30.2	15.1
Tree condition						
Living	43.5	59.0	65.8	85.1	94.1	96.7
Dead	56.5	41.0	74.2	14.9	5.9	3.3
Foraging place						
Trunk	34.8	73.5	21.4	72.4	92.3	77.9
Large branches	24.5	11.0	6.0	8.6	6.2	8.6
Medium branches	29.0	4.7	11.9	10.5	0.7	0.9
Small branches	11.7	10.8	60.7	8.5	0.8	12.6
Foraging technique						
Gleaning	8.9	13.9	84.2	32.9	95.1	90.7
Probing	2.7	17.6	10.7	36.3	4.9	9.3
Scaling	8.1	48.8	5.1	30.2	–	–
Excavating	12.3	19.7	–	–	–	–
Husking	60.8	–	–	0.3	–	–
Picking up cones	5.9	–	–	–	–	–
Earth gleaning	1.3	–	–	0.3	–	–

3.2. Microhabitat utilizations and foraging techniques

All information concerning microhabitat utilization and foraging technique variables are given in Table 3. Different guild members demonstrated clearly diverse patterns of resource utilization. It was expressed mostly in foraging techniques, since only *D. major* used all distinguishable foraging categories. In fact, *D. major* was the only species which also utilized other sources of food than bark, i.e. pine-cones. In the case of other microhabitat utilization variables, all the distinguishable categories were used by all species. However, it is clear that different species seem to prefer different tree species, trees in different conditions or different foraging places (Table 3).

Table 4. Principal component analysis of locomotion and microhabitat utilization variables for six coexisting bark-foraging species with varimax factor loadings. Only the highest factor loadings (> 0.5) for each variable are shown (see Table 2 for abbreviations).

Statistics	Principal component factors 1	2	3	4
Eigenvalue	3.81	2.57	2.47	1.76
% of variance	17.3	11.7	11.2	8.0
Cumulative %	17.3	29.0	40.3	48.2

Variables	Rotated factor loadings			
TF	–	–	–	0.60
H_1	–	–	0.73	–
H_2	–	–	0.80	–
LM	0.91	–	–	–
SPEED	0.75	–	–	–
LF	–	–	–	–
TRESPE – Scotch Pine	–	0.88	–	–
TRESPE – Oak	–	–	–	0.61
TRESPE – other	–	–	0.51	–
TRECON – living	–	–	–	–
TRECON – dead	–	–	–	–
FORPLA – trunk	–	–	–	–
FORPLA – ∅ > 10 cm	–	–	–	–
FORPLA – ∅ 5–10 cm	–	–	–	–
FORPLA – ∅ < 5 cm	–	–	–	–
FORTEC – gleaning	0.68	–	–	–
FORTEC – probing	–	–	–	–
FORTEC – scaling	–	–	–	0.73
FORTEC – excavating	–	–	–	–
FORTEC – husking	–	0.74	–	–
FORTEC – picking cones	–	–	–	–
FORTEC – earth gleaning	–	–	0.61	–

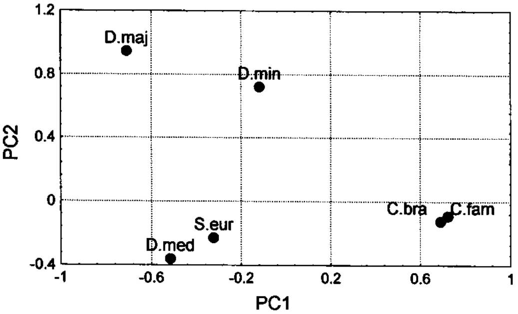

Fig. 1. Location of the studied species in the PC1 and PC2 ecological factors obtained by applying PCA.

3.3. Principal component analysis of locomotion and microhabitat utilization variables

Nine principal components were derived by the PCA from the correlation matrix of 22 locomotion and microhabitat utilization variables (Table 4). The first four were compound variables, while the others had very limited explanatory power and were omitted from the analysis. All these compound variables were highly correlated with some locomotion variables taken under analysis (Table 4). Fig. 1 shows the position of the species along the first two PCA axes based on ecological data. PC1 was a "movement's length and speed" and a "gleaning use" component which strongly separated both treecreepers from the other species. PC2 separated *D. major* from the rest of the species as it was connected with cone exploitation. PC3 was mainly a "horizontal tree axis" separating passerines and woodpeckers from each other (Table 4, Fig. 2). PC4 separated *D. medius* from the rest of the species.

Considering all locomotion variables, only *Certhia* spp. demonstrated really similar locomotion patterns (Fig. 3). In other species some crucial differences were always confirmed. Albeit most variables differentiated woodpeckers and passerines, they did not form strictly separate groups (see Tables 2 and 5).

3.4. Size vs. locomotion patterns and foraging behaviour

Size was correlated with the majority of the locomotion variables and with two principal components (i.e. PC1 and PC4, Table 6). It indicates that such variables of locomotion pattern as LM,

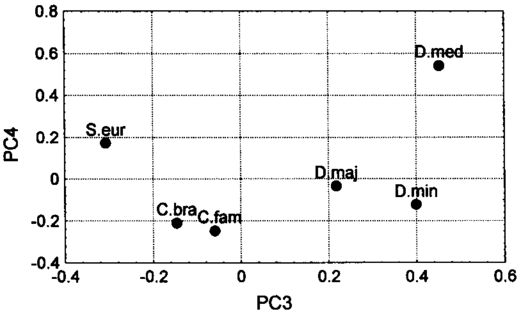

Fig. 2. Location of the studied species in the PC3 and PC4 ecological factors obtained by applying PCA.

SPEED, TF and DS ratio were strongly determined by size. Length of flight was not associated with size or any microhabitat utilization variable, and formed a separate principal component which did not carry any additional information other than length of flight. H_1 was significantly positively related to size, while in the case of H_2 such a relationship was insignificant (Table 6). PC3 was positively correlated to both indexes of foraging height (H_1 and H_2) but it was not related significantly to size (Tables 4 and 6).

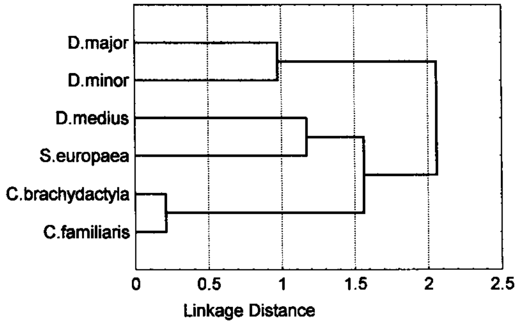

Fig. 3. Cluster of affinities (unweighted pair-group average method and Euclidean distances) based on 9 principal components describing locomotion and foraging of six bark-foraging species.

4. Discussion

Woodpeckers, nuthatches and treecreepers partly exploit the same resources. However, because they exhibit a different morphology, with body-size differentiation as a crucial factor, they do not have the same predispositions to microhabitat utilization. The results obtained confirm earlier studies (Spring 1965, Storer 1971, Winkler & Bock 1976, Jenni 1981, Norberg 1986, Carrascal et al. 1990, Matthysen 1990, Moreno 1991, Raikow 1994) as the majority of components connected with locomotion pattern were strongly associated with size. If we take into consideration the locomotion patterns in woodpeckers only, they were exactly the same as found by Jenni (1983), Vanicsek (1988) and Török (1990), and mobility increased with decreasing body-size of the species.

Different members of the studied guild use separate trees as single- or multipatched places of

Table 5. Number of significant ($P < 0.05$) differences between pairs of species within and between woodpecker and passerine groups tested by post hoc Newman-Keuls test (see Table 2 for abbreviations).

Variable	Within woodpeckers	Within passerines	Between woodpeckers & passerines
TF	2	0	3
H_1	1	3	9
H_2	1	2	9
LM	2	2	8
SPEED	3	3	8
LF	2	3	8
PC1	3	2	9
PC2	3	2	9
PC3	1	2	9
PC4	2	2	7
No. pairs tested	3	3	9

Table 6. Spearman rank correlation coefficients (r_s) and their significances, between size and locomotion variables (n = 6 species).

Variable	Size
Mean time of foraging on tree (sec)	0.83 *
Mean length of movements (m)	– 0.89 *
Mean initial height of movement (m)	0.89 *
Mean final height of movement (m)	0.49 ns
Ratio of foraging with dynamic and stationary pattern	– 0.83 *
Mean speed of movements (m/min)	– 0.85 *
Mean length of flights (m)	0.31 ns
PC1	– 1.00 ***
PC2	0.03 ns
PC3	0.37 ns
PC4	0.83 *

ns: not significant; * $p < 0.05$; ***: $p < 0.001$

foraging to different degrees (see DS ratio in Table 2). This is one of the most important factors separating bark foragers. *D. major,* in most cases, use only one place on a tree, which can be exploited without or almost without any movement along the trunk or branches. In contrast, the locomotion pattern of both treecreepers showed use of the trunks and/or branches as a group of many small patches. This kind of pattern involves movement. However, a similar DS ratio does not directly mean that species apply similar locomotion strategies. For example, *D. major* and *D. minor* showed similar foraging patterns considering the DS ratio, but were, in principle, different in their locomotion habits. *D. major* was a slow creeper making only short trips along trunks and branches while *D. minor* was a fast creeper with almost double the mean length of movements (see Vanicsek 1988, Török 1990). On the other hand, *D. minor* differed from both *S. europaea* and *Certhia* spp., even though these species were also very mobile.

There is a positive relationship between the speed of movements and energy expenditure (Schmidt-Nielsen 1994). Energy input depends on the number of food items found and this number is connected with (1) the distribution of food, which is often patchy, and (2) speed, as the probability of overlooking an item is a function of speed (Holling 1959, Stephens & Krebs 1986). Therefore, when foraging techniques with similar handling times are applied, the speed of movements should be related to microhabitat quality and should be lower in microhabitats with higher food abundance. Consequently, alternate food resources should involve different strategies. In light of these facts, the interpretation of interspecific differences is much simpler.

Search speed and search costs may affect prey and patch decisions (DeBenedicts et al. 1978, Schmid-Hempel et al. 1985). Thus, both length of movement and speed of creeping depend on the microhabitat and foraging techniques used. Long movements were specific for treecreepers, which mainly glean on trunks of living trees (Vanicsek 1988, Cuisin 1990). It is necessary to remember that this microhabitat is very low in production and that arthropod food is not a renewable source during winter (Dziabaszewski 1976, Török 1990). Therefore, treecreepers utilize trunks in a very efficient way. Maximizing the movement length and spiral types of movements allows the bird to check the greatest number of potential prey hiding places. Cuisin (1990) showed that Short-toed treecreepers check up to 30% of the potential tree surface, which is remarkably more than other bark-foraging species do.

On the other hand, the behaviour of *Certhia* sp. contrasted with the locomotion pattern of *D. minor.* This small woodpecker crept significantly faster than treecreepers, if we considered only foraging with a dynamic pattern (Osiejuk unpubl.). However, it rarely used such a mobile pattern (see DS ratio in Table 2). My observations suggest that the difference between the locomotion of *Certhia* spp. and *D. minor* is that *Certhia* spp. was looking for food items during movements while *D. minor* simply moved from one food patch to another without looking for food. Treecreepers probably are able to detect single arthropods from only a very short distance, while *D. minor*'s strategy depends on detecting possible food patches (projecting bark pieces) from a greater distance. Therefore, treecreepers should balance creeping speed with due regard to the risk of overlooking prey items, while *D. minor* should creep fast in order to reduce the time of movements (see Southwood 1961, Jenni 1983, Török 1990 and also patch and prey average-rate maximizing models presented in Stephens & Krebs 1986). One could thus explain the differences in the locomotion strategy of *D. minor* and *Certhia* spp. as a direct effect of different microhabitat exploitation caused by morphological adaptations.

Treecreepers are very specialized species and exploit only the bark surface. This explains why their only strategy is relatively easier to describe on the basis of the foraging theory. Other species could apply more than one feeding strategy and switch between them.

Similarly, in the case of *S. europaea,* we have to distinguish more than one foraging strategy. This generalist species used, to some extent, three foraging techniques where timing could be easily explained in terms of a relation between time of foraging and food resource accessibility. There is one important conclusion resulting from this section. Specialized species (i.e. treecreepers) should have similar locomotion patterns in different areas, while generalists could show more than one locomotion pattern in different areas since they could apply their specific foraging strategies in various proportions depending on local conditions (compare with Hogstad 1978, Conner 1981, Vanicsek 1985, Szekely 1987, Török 1990, Osiejuk 1994).

Foraging time was very diverse both among bird species and among ecological variables. Generally, TF should be longer when birds exploit rich, aggregated food resources or when food is hard to reach (Jenni 1983, Aulén 1988, Török 1990, Aulén & Lundberg 1991). Patterns found in this study match well with this idea. For example, in *D. major* and *D. medius*, mean TF for excavating was longer in comparison with probing and scaling (Table 7). In other more mobile species, foraging time was modified not only by the technique applied but also by the number of patches per tree which were exploited. Focusing on separate species leads to the conclusion that foraging techniques requiring more energy and stronger feeding structures (mainly bill and head construction), also took more time. In other words, foraging techniques mostly influence interspecific foraging time differentation, because techniques are directly related to handling time.

However, I found that foraging time is primarily related to the foraging technique applied. An important consequence of mean time spent on one tree is the number of flights per unit time which may influence the risk of predation. If more flights increase the predation risk, species more exposed to danger of predation during the flight should limit the frequency of flights. In the study area, the most often observed predator was the Northern Goshawk *Accipiter gentilis*, which preferred larger species from among the studied guild. The data obtained in the study show that the larger species tended to have low flight frequency but this relation was not significant. However, this hypothesis requires a specifically designed experiment for verification.

The length of flights was not related to size or any microhabitat utilization variable. The logical factors which could influence LF are the pattern of tree species use and the distribution of trees. This means that generalist species should have a shorter mean LF than specialized species which choose more dispersed tree species. The percentage of different tree species used, support such a hypothesis for all species (especially if TRESPE — other category is divided into particular tree species, Osiejuk unpubl.). Passerines, which used a wider selection of tree species, had significantly shorter flights than woodpeckers, which preferred pines (*D. major*) or oaks (*D. medius* and *D. minor*). However, if we exclude *D. minor* from the analysis it appears that the differentiation of LF is also highly related to size.

The differences between woodpecker and passerine locomotion patterns were not so clear. The most distinct difference between woodpeckers and passerines is that the first group started and finished foraging higher in the tree than the second group. Woodpeckers also had a longer mean length of flight. Because two of these variables (i.e. H_2 and LF) were not connected significantly with size, one could suppose that the difference between woodpeckers and passerines was not caused by size-originating factors. In fact, in both groups, size dimension is not the only factor that is not uniform. The two groups are also not uniform in their foraging. In passerines, two species have a very similar climbing technique (i.e. treecreepers), while the Eurasian Nuthatch is completely different because it does not use the tail as

Table 7. Mean foraging time TF ± SD of six studied species foraging with bark and wood exploiting techniques. Techniques ordered according to increasing energy expenditure.

Species	Gleaning	Probing	Scaling	Excavating
Dendrocopos major	49 ± 64	197 ± 133	148 ± 97	287 ± 209
Dendrocopos medius	24 ± 24	77 ± 67	142 ± 89	172 ± 69
Dendrocopos minor	47 ± 41	34 ± 22	56 ± 18	–
Sitta europaea	35 ± 46	94 ± 67	128 ± 83	–
Certhia brachydactyla	73 ± 99	145 ± 31	–	–
Certhia familiaris	61 ± 67	117 ± 34	–	–

In all species mean differences between foraging techniques were significant (ANOVA, P < 0.001).

a supporting structure (Jenni 1981, Norberg 1986, Carrascal et al. 1990, Moreno 1991). In woodpeckers, *D. major* spent more than half of its total foraging time feeding on cones (total time of picking up cones and husking). Other species did not use this food source at all. This clearly resulted in a deviating locomotion pattern for *D. major* compared with other woodpeckers. Additionally, the bill structure is very diverse between and within these two groups. On the other hand, *D. minor* and *S. europaea* belong to different systematic groups, but some locomotion pattern aspects may be more similar simply because they are similar in size. The differences in size are also greater in woodpeckers than in passerines. In fact, only the treecreepers had very similar locomotion patterns (Fig. 3).

The differences between treecreepers' locomotion variables were small except SPEED, LF and H_1. If we compare these results with microhabitat utilization of both *Certhia* sp. the conclusion is that differences in treecreepers' locomotion patterns arise from feeding niche differentiation. Is this differentiation related to morphology divergence (bill length, hind claw length) or social interaction? For now, this question remains unanswered.

5. Concluding remarks

Species mobility was inversely related to body-size within the bark-foraging guild. It was confirmed by the majority of relations between size and locomotion variables. This general pattern was strongly modified by factors other than size. Some morphological factors may influence locomotion directly (flying and climbing techniques — see Norberg 1986, Matthysen 1990, Moreno 1991), and some indirectly influence locomotion (for example, bill shape affects foraging techniques, which are related to length of movement and foraging time).

All species studied, except treecreepers, applied more than one foraging strategy. Hence, their specific locomotion patterns presented here are essentially the result of several overlapping real patterns.

Woodpeckers and passerines did not form strictly separate groups on the basis of locomotion differentiation. Based on all principal components, only treecreepers were really similar in locomotion patterns.

Differences between locomotion patterns of *C. brachydactyla* and *C. familiaris* concerned creeping speed and length of flight, and seem to be an effect of different microhabitat utilization, especially in tree species and foraging place dimensions.

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Selostus: **Puun rungolla ruokailevien lintujen ravinnon hankinta talvella**

Kirjoittaja tutki puun rungolla ruokailevien kolmen tikkalajin (käpy-, tammi- ja pikkutikka) ja kolmen varpuslintulajin (pähkinänakkeli, puukiipijän ja etelänpuukiipijä) ravinnon hankintakäyttäytymistä. Tutkimus tehtiin Länsi-Puolassa viiden talven aikana (1990–95). Tutkimuksen tarkoitus oli kuvata näiden lajien ruokailukäyttäytymistä ja etenkin ruokailun aikana tapahtuvia liikkumisia. Lajien väliset erot käyttäytymisessä ja liikkumisessa ruokailun aikana ovat mahdollisesti tärkeitä tekijöitä vähentämään lajien välistä kilpailua uusiutumattomista, rajallisista talviravintovaroista. Liikkuvuutta tutkittiin myös suhteessa lajin kokoon.

Lajien liikkuvuudessa ruokailun yhteydessä oli suuria eroja (Taulukko 2). Suurikokoiset lajit liikkuivat vähemmän rungolla ollessaan, ruokailivat enemmän paikallaan ja tekivät lyhyempiä siirtymisiä rungolta toiselle kuin pienikokoiset lajit (Taulukko 6). Suurikokoiset lajit viettivät myös pidempiä aikoja yhdellä rungolla, mikä on yhteydessä suurikokoisten (tikka-)lajien ruokailutapaan kaivaa ravintoa kaarnan alta tai rungosta (Taulukko 3). Tikat ja varpuslinnut eivät kuitenkaan muodostaneet selkeitä, erillisiä ruokailutaparyhmiä. Esimerkiksi pähkinänakkeli ja tammitikka olivat ruokailukäyttäytymisessään hyvin samanlaisia (Kuvat 1 ja 3). Kaksi puukiipijälajia olivat ravinnonhankitakäyttäytymisessään hyvin samanlaisia mutteivät kuitenkaan identtisiä. Nämä lajit poikkesivat toisistaan mm. siinä, että puukiipijä ruokaili enemmän männyillä kuin etelänpuukiipijä, joka näytti suosivan tammea ja muita lehtipuita ruokaillessaan (Taulukko 3).

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