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Komárek O., Sukačová K.: Použití umělých substrátů v různých růstových podmínkách.

Cílem této studie bylo srovnání přirozených a umělých substrátů pro získání maxima informací o vhodnosti materiálů blízkých přírodním pro hodnocení znečištění vody v tocích. Použité umělé substráty jsou hranaté desky z čerstvě nalámané žuly. Tyto byly vloženy do říčního koryta a exponovány v různých časových intervalech. Čerstvý žulový materiál má několik omezení pro růst perifytonu a indikaci znečištění vody. Z těch nejdůležitějších jsou to různě rychlá sukcese a rozdílné podmínky na lokalitách. Výzkum byl prováděn na čtyřech lokalitách a zahrnoval charakteristiku biotopu, druhové složení a semikvantitativní druhovou abundanci doplněnou o chemická data. Ordinační statistické metody byly použity pro hodnocení indikační schopnosti této metody. Z výsledků vyplývá, že je nevhodné použití umělých substrátů pro určení znečištění v podmínkách nevhodných pro dostatečně rychlý rozvoj společenstva. Možným řešením je instalace substrátů celý rok před vlastním hodnocením, což umožní vyrovnat sukcesní rozvoj. CCA je dobrou metodou pro testování možnosti použít umělé substráty ve specifických podmínkách.

METABOLIC RATES IN PASSERINE BIRDS: EFFECTS OF ADAPTIVE STRATEGIES AND TAXONOMY

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Abstract

Cierlik G., Tworek S., Makomaska-Juchiewicz M., Profus P.: Metabolic rates in passerine birds: effects of adaptive strategies and taxonomy. Ekológia (Bratislava), Vol. 23, No. 2, 207-224, 2004.

The hypothesis that the metabolic rates of birds are convergent and depend on functional adaptations was tested as an alternative that taxonomic affiliations sufficiently account for variation in metabolism. Basal metabolic rates (BMR) of 122 species from six families (*Corvidae*, *Emberizidae*, *Fringillidae*, *Muscicapidae*, *Nectariniidae*, and *Parulidae*) of passerine birds were taken from literature and compared with data on their life history traits: food habits, climate, habitat, biotope, type of nest and migrations. Using factor analysis and clustering procedures different strategies were distinguished according to assortment of traits – food strategies: “nectarivorous”, “insectivorous”, “granivorous”, “omnivorous”; environmental strategies: “terrestrial”, “tropical”, “boreal” and strategies based on analysis of food and remaining traits together: “group 1”, “group 2”, “group 3”. These sets are only partly congruent with taxonomic classification. All groups demonstrate similar dependence of BMR on body weight but “granivorous” have a significantly higher BMR than “nectarivorous” and “tropical” has lower BMR than “terrestrial” and “boreal”. In contrast, *Fringillidae* have significantly higher BMR than *Muscicapidae*, *Emberizidae*, *Nectariniidae* and *Parulidae*. Analysis of residuals within ANCOVA for strategies and for families indicates that taxonomic affiliation exerts greater influence on BMR values than adaptive strategy.

Key words: passerine birds, metabolic rates, functional adaptations, taxonomic affiliation, life strategy

Introduction

Relationships between metabolic rate and body mass in birds have been studied by many authors (e.g. Lasiewski, Dawson, 1967; Calder, 1984; Scott et al., 1996) and nowadays it is generally known that this dependence accounts for most of the interspecific variation of metabolism. The residual variation (with regard to body mass effect), however, is still enormous and demands explanation. Some authors checked which species have metabolic rate

higher or lower than expected for such a body size and whether this variation is connected with differences in their ecology and behaviour (Vleck, Vleck, 1979; Walsberg, 1983). With reference to energy budgets of birds and mammals McNab (1974, 1988) postulated the existence of connection between metabolic rate and some components of life strategy such as food habit, climate or habitat. For example, the birds feeding on insects on the wing (swallows, swifts) have low basal metabolic rate and tendency to use torpor, whereas the birds feeding on larvae (woodpeckers, tits) have usually high BMR (McNab, 1974). Desert animals have relatively low BMR, which may be an adaptation for climate (Weathers, 1979). All these arguments are based on the implicit assumption that the basal metabolic rate, a laboratory measurement taken in extremely artificial conditions, does scale up to actual metabolic rate in the field, which in turn reflects the energetic costs of certain functional adaptations. This assumption can hardly be proved, because field energy budgets have been computed for only a few bird species and these estimates demonstrate difficulty in explaining variation (e.g. Nagy, 1987; Bryant, Tatner, 1988; Williams et al., 1991). In the case of birds, the correlation between basal and field metabolic rates or between BMR and daily energy expenditure is usually significant, although not in all tests (Koteja, 1991; Gavrilov, 1996; Ricklefs et al., 1996; Cooper, 2000) and this relationship should be examined on larger material.

On the other hand, species belonging to one taxonomic group are very likely to have similar habits and other authors suggest that most of the variation in metabolism may be attributed to taxonomy rather than to life history traits which may be both convergent and homologous traits. Harvey and collaborators (Bennett, Harvey, 1987; Elgar, Harvey, 1987), using their own methods of statistical inference (Pagel, Harvey, 1988, Harvey, Pagel, 1991) did not find any significant correlation between the basal metabolic rate and life history traits that could not be attributed solely to taxonomy and body size. A distinction between the energetic costs of functional adaptations and the effects resulting from the conservative traits of a species, which constitute its phylogenetic heritage, is a stiff issue in any comparative evolutionary study. A good example is the comparison of species-specific metabolic rates and the choice of proper methodology is still intensively discussed (Harvey, Elgar, 1987; McNab, 1987; Pagel, Harvey, 1988; Harvey, Pagel, 1991; Stearns, 1992; Reynolds, Lee, 1996).

Most previous analyses dealt with single traits (food habits, habitat, climatic preference). But some traits are positively or negatively correlated with each other. A number of feasible combinations is huge. Such combinations, and not the single traits, are subject to natural selection and constitute the adaptive strategies of the species. This may obscure any possible functional relationships, for example between food habits and energetic costs. The problem was recognised among mammals. McNab (1989) treated different traits simultaneously in the analysis of BMR variance in carnivorous mammals. He partitioned the total variation into the effects depending on body weight, climate, activity and food habits, using a sequential analysis of regression standard errors. Then Koteja, Weiner (1993) on the basis of four traits: food habit, climate, habitat and biotope, distinguished three separate strategies of murid rodents, which are different from taxonomic affiliation. They con-

firmed the hypothesis that functional adaptations influence the BMR values in murid rodents, independently of taxonomy.

Our aim was to analyse potential energetic costs of various life styles in birds, bearing in mind the inherent drawbacks indicated above. One of the best ways to isolate functional adaptations from phylogenetic similarities is to make comparisons within rather than across the taxa (Pagel, Harvey, 1988). Passerine birds, a phylogenetically narrow group but consisting of many species with a large spectrum of ecological adaptations, seems to fulfil the requirements of such a comparative study. To cope with the problem of correlated traits we described the adaptive strategy of passerine birds by selecting the groups of species showing similar adaptations to environmental factors, so-called environmental variables (i.e. climate, habitat, biotope, nest), food habits and for all the variables together. To find any differences in energetic costs we compared whole strategies, using body-size-controlled metabolic rates, averaged for groups of species representing similar life styles.

Material and methods

Data on metabolic rates of passerine birds have been taken from literature. To avoid errors connected with various standards of measurements, we used only values reported by the authors as basal metabolic rate (BMR), or values that fulfilled the usual requirements for BMR measurement (adult animals at rest under postabsorptive conditions in a thermoneutral environment). We accepted the taxonomic classification of Morony et al. (1975) and the six most numerous represented families (122 species) were chosen for statistical analysis: 14 *Corvidae*, 23 *Emberizidae*, 21 *Fringillidae*, 34 *Muscicapidae*, 15 *Nectariniidae* and 14 *Parulidae*. The numbers of species in the groups are accidental and reflect the availability of data in the literature. The proportions of data collected to the described number of species in the groups oscillate from 5% (*Muscicapidae*), through 13-16% (*Parulidae*, *Emberizidae*, *Corvidae*, *Nectariniidae*) to over 20% (*Fringillidae*). In most cases the original publications were used (see Appendix and References).

Information on the life style of a given species was collected from various sources: monographic publications were preferred to general reviews. The selection and categorization of variables was dictated partly by the choice of data available in the literature. Analyses were effected on six species-specific traits: food habits, climate in the typical area of distribution, habitat preferences, biotope, type of nest and migration. These traits were grouped and ranged as follows:

1. Food habits – this trait was treated unlike the others because in many cases it is hardly possible to univocally qualify the food taken by birds. We distinguished seven types of food of the passerine birds (green parts of plants, fruits and berries, seeds, nectar, anthropogeneous food, invertebrates, vertebrates and carrion). For each species we tried to assess the significance of particular foods in its diet using four categories: the food is absent in diet, addition, main food, the only food.
2. Climate – according increasing temperature and decreasing seasonality.
3. Habitat preferences – from terrestrial through various layers of vegetation to feeding on the wing.
4. Biotope – from open, desert and least productive to moist with dense vegetation.
5. Nest – from open, under the greatest pressure of predators to hidden in hollows and burrows.
6. Migration – from residents to regular vagrants.

These variables except for type of food were quantified on an arbitrary linear scale according to gradients mentioned above: biotope from 1 to 6, climate and migration from 1 to 5, whereas habitat and nest, from 1 to 4. Food habits were described from 0 to 3 as mentioned above. Thus, twelve numbers defining environmental preferences described each species. Multivariate analysis was applied to these data to separate various life strategies. Factor analysis and K-means cluster analysis for the distinguished factor scores were employed.

Table 1. Factor analyses

A. Food: factors are the first three principal components Varimax rotated

Variables	Factors		
	1	2	3
	Rotated loadings		
Plants	0.388	0.216	-0.487
Fruit	0.093	-0.153	-0.806
Seeds	0.040	-0.905	-0.276
Nectar	0.005	-0.190	0.802
Anthropogeneous food	0.871	0.069	-0.064
Invertebrates	-0.003	-0.914	-0.114
Vertebrates	0.858	-0.067	-0.082
Percent of total variation explained	31.6	23.3	17.3

B. Climate, habitat, biotope, nest: factors are the two first principal components Varimax rotated

Variables	Factors	
	1	2
	Rotated loadings	
Climate	-0.029	-0.905
Habitat	0.794	-0.287
Biotope	0.856	0.091
Nest	0.480	-0.559
Percent of total variation explained	46.1	24.4

C. All variables. Factors are the first three principal components Varimax rotated

Variables	Factors		
	1	2	3
	Rotated loadings		
Plants	0.469	0.334	0.182
Fruit	0.306	0.577	-0.175
Seeds	0.079	0.204	0.902
Nectar	-0.177	-0.834	-0.228
Anthropogeneous food	0.803	-0.059	0.061
Invertebrates	0.110	0.120	-0.846
Vertebrates	0.833	0.065	-0.027
Climate	0.190	-0.650	-0.205
Habitat	-0.450	-0.363	-0.578
Biotope	-0.378	-0.147	-0.473
Nest	-0.083	-0.577	-0.392
Migration	-0.403	0.676	-0.328
Percent of total variation explained	29.4	17.9	13.9

Hypotheses about the metabolic effects of various life strategies and, alternatively, of different taxonomic affiliation were tested by analysis of covariance. Basal metabolic rates were regressed on body weights, after logarithmic transformation of both variables. The significance of differences in regression coefficients was tested by analysis of covariance, separately for clusters representing various strategies and for taxonomic groups. For each of the two data arrangements the dependence of residuals on the remaining classification was tested by simple analysis of variance. The Bonferroni method for multiple comparisons was applied a posteriori.

Results

Factor analysis and cluster analysis – Three factors have relatively high loading and a plausible interpretation if food variables are taken into account (Table 1A). Each of them has significance in cluster analysis (Table 2A). The studied set of birds split into four groups with clearly different food strategies. The first group consists of 13 species of *Nectariniidae*; the second of 31 *Muscicapidae*, 14 *Parulidae*, 6 *Emberizidae* and 2 *Nectariniidae* (*Anthreptes collaris*, *Anthreptes orientalis*) and *Garrulus glandarius* (*Corvidae*); the third of 20 *Fringillidae*, 16 *Emberizidae* and 2 *Corvidae* (*Nucifraga caryocatactes*, *Perisoreus canadensis*); and the fourth of 12 *Corvidae*, 3 *Muscicapidae* and *Emberiza citrinella* (*Emberizidae*), and *Carpodacus cassinii* (*Fringillidae*). The complete list of species in each group is given in Appendix. For simplicity we refer to these groups as “nectarivorous”, “insectivorous”, “granivorous” and “omnivorous”, although the species in each group feed sometimes in a different manner as compared with the typical of the name.

Two factors have relatively high loadings, making further interpretation possible if climate, biotope, habitat and nest are taken into account (Table 1B). Both have a similar significance in cluster analysis (Table 2B). In this case the studied group of birds split into three strategies (Appendix). The first, with 11 species of *Corvidae*, 12 *Emberizidae*, 4 *Fringillidae*, 3 *Muscicapidae* and *Seiurus aurocapillus* (*Parulidae*); the second, with 15 *Nectariniidae*, 10 *Muscicapidae*, 5 *Parulidae*, *Cardinalis cardinalis* (*Emberizidae*) and *Serinus canaria* (*Fringillidae*); and the third, with 21 *Muscicapidae*, 16 *Fringillidae*, 10 *Emberizidae*, 8 *Parulidae* and 4 *Corvidae*. For simplicity we refer to these groups as “terrestrial”, “tropical” and “boreal” although such names reflect only partly environmental preferences of the birds belonging to those groups.

Three factors are important for further interpretation if all the variables are taken into account (Table 1C). All of them are significant in clustering (Table 2C) which divides species into three groups. The first consists of 21 *Fringillidae*, 21 *Emberizidae*, 14 *Corvidae* and *Turdus merula* (*Muscicapidae*); the second is formed by 31 *Muscicapidae*, 14 *Parulidae*, 2 *Emberizidae* (*Plectrophenax nivalis*, *Zonotrichia georgiana*) and *Garrulus glandarius* (*Corvidae*); and the third, by 15 *Nectariniidae* and 2 *Muscicapidae* (*Copsychus saularis* and *Hypothymis azurea*). In a three-dimensional space delimited through the factors the groups are distinctly separated, which is also seen in two-dimensional figures. When plotted, the scores of factors 1 and 2 for each species clearly show a separate character of *Nectariniidae* in relation to the others (Fig. 1).

Table 2. Clustering

A. Food variables

Factors		1	2	3
Group	n	Factor scores \pm SD		
"Nectarivorous"	13	-0.02 ± 0.00	-0.44 ± 0.40	2.33 ± 0.12
"Insectivorous"	54	-0.44 ± 0.22	-0.75 ± 0.47	-0.41 ± 0.56
"Granivorous"	38	-0.38 ± 0.28	1.21 ± 0.56	-0.09 ± 0.63
"Omnivorous"	17	2.25 ± 0.95	0.01 ± 0.72	-0.28 ± 0.75
F		200.8	103.7	77.9

B. Climate, habitat, biotope, type of nest

Factors		1	2
Group	n	Factor scores \pm SD	
"Terrestrial"	31	-1.35 ± 0.56	-0.53 ± 0.54
"Tropical"	32	1.03 ± 0.55	-0.95 ± 0.75
"Boreal"	59	0.15 ± 0.45	0.79 ± 0.60
F		180.4	93.8

C. All variables

Factors		1	2	3
Group	n	Factor scores \pm SD		
Group 1	57	0.37 ± 1.29	0.08 ± 0.52	0.90 ± 0.66
Group 2	48	-0.31 ± 0.41	0.63 ± 0.50	-0.82 ± 0.43
Group 3	17	-0.37 ± 0.59	-2.03 ± 0.60	-0.69 ± 0.41
F		8.2	164.0	144.4

Metabolic rates – The linear regression of BMR on body size calculated for 122 species of passerine birds belonging to six families has an exponent 0.744 and accounts for 95% of the total variation in BMR. Regression lines, fitted to the data grouped by various classifications: taxonomy, food strategy and environmental strategy, differ only slightly and not significantly in the exponents ($p > 0.05$). However, for repartition based on all the variables together the differences in the exponents are statistically significant ($p < 0.05$). The percentage of the variation explained by body mass varies in different groups from 69% to 98% (Table 3).

Analysis of covariance demonstrates statistically significant differences among families and among strategies (Table 4, $p < 0.001$): *Fringillidae* have distinctly higher metabolic rates than other families, "granivorous" have higher metabolic rates than "nectarivorous" and "tropical" have lower metabolic rates than "terrestrial" and "boreal". When all the variables are taken into account, ANCOVA reveals statistically significant differences in the slopes of linear regressions between strategies ($p < 0.001$, Table 4D).

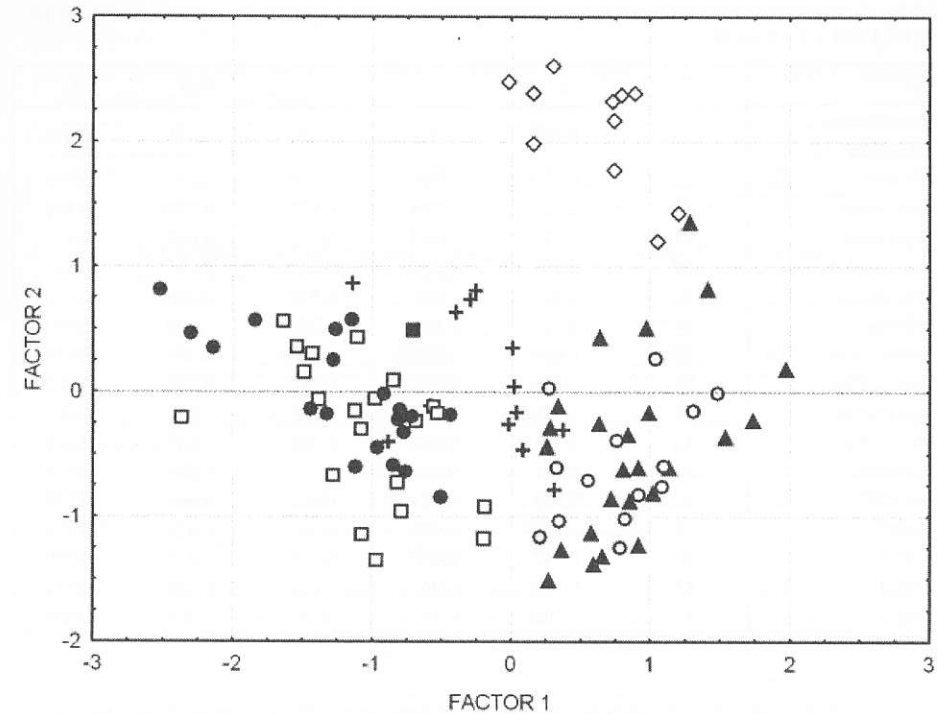


Fig. 1. The scores of Factor 1 and Factor 2 plotted for 122 species of passerine birds. Symbols correspond to taxonomic affiliation: + = *Corvidae*, □ = *Emberizidae*, ● = *Fringillidae*, ▲ = *Muscicapidae*, ◇ = *Nectariniidae*, ○ = *Parulidae*.

Taking the distinguished strategies into account, the residuals from the regression lines for food strategies and environmental strategies depend on taxonomy, with *Fringillidae* tending to have higher metabolic rates than other passerines. On the other hand, if the species are ordered in accordance with the taxonomic affiliation, the residuals are still significantly correlated with the food strategy or the environmental strategy of the species: "granivorous" tend to have higher metabolic rates than "nectarivorous" and "tropical" have lower metabolic rates than "boreal" and "terrestrial" (ANOVA, $p < 0.01$, Table 5).

Discussion

The values of the linear regression of BMR on body size are similar to other estimates for passerine birds (Bennett, Harvey, 1987). However, degrees of correlation between log BMR and log body weights vary in particular groups. In *Corvidae* and in the groups with a large number of species from this family the exponent reaches the highest values. That means

Table 3. Regressions of basal metabolic rates (BMR, kJ/d) on body weight (W, g) in passerine birds of the form $\log \text{BMR} = a + b \log W$

Item	N	a	SEa	b	SEb	R ²
<i>Passeriformes</i> – 6 families	122	0.463	0.022	0.744	0.015	0.954
<i>Corvidae</i>	15	0.512	0.066	0.715	0.027	0.982
<i>Emberizidae</i>	23	0.354	0.095	0.820	0.070	0.866
<i>Fringillidae</i>	21	0.575	0.069	0.719	0.049	0.919
<i>Muscicapidae</i>	34	0.507	0.070	0.715	0.055	0.842
<i>Nectariniidae</i>	15	0.641	0.088	0.517	0.086	0.734
<i>Parulidae</i>	14	0.421	0.084	0.736	0.080	0.875
“Nectarivorous”	13	0.627	0.090	0.534	0.088	0.771
“Insectivorous”	54	0.400	0.044	0.792	0.036	0.902
“Granivorous”	38	0.529	0.062	0.723	0.044	0.882
“Omnivorous”	17	0.395	0.094	0.762	0.041	0.958
“Terrestrial”	31	0.518	0.040	0.716	0.021	0.975
“Tropical”	32	0.559	0.073	0.612	0.068	0.731
“Boreal”	59	0.474	0.037	0.751	0.026	0.934
Group 1	57	0.547	0.029	0.706	0.017	0.970
Group 2	48	0.436	0.043	0.765	0.035	0.914
Group 3	17	0.706	0.081	0.442	0.077	0.689

Table 4. Regressions of basal metabolic rates (BMR) on body weight (W) in passerine birds: analyses of covariance. Groups underlined do not differ significantly ($p > 0.05$)

A. Grouping by taxonomy (families): 1 – *Fringillidae*, 2 – *Corvidae*, 3 – *Muscicapidae*, 4 – *Emberizidae*, 5 – *Nectariniidae*, 6 – *Parulidae*

Group	1	2	3	4	5	6
Intercept	<u>0.582</u>	<u>0.517</u>	0.509	0.496	0.445	0.444

B. Grouping by food strategies: 1 – “granivorous”, 2 – “insectivorous”, 3 – “omnivorous”, 4 – “nectarivorous”

Group	1	2	3	4
Intercept	<u>0.488</u>	<u>0.446</u>	<u>0.415</u>	0.407

C. Grouping by environmental strategies (based on four variables: climate, habitat, biotope, type of nest): 1 – “boreal”, 2 – “terrestrial”, 3 – “tropical”

Group	1	2	3
Intercept	<u>0.517</u>	<u>0.512</u>	0.444

D. Grouping by strategies based on all variables: 1 – group 1, 2 – group 2, 3 – group 3

Group	1	2	3
Slope	<u>0.706</u>	<u>0.765</u>	0.442

Table 5. Analyses of variance for residuals from ANCOVA regressions. Groups underlined do not differ significantly ($p > 0.05$)

Taxonomic families within food strategy groups: 1 – *Parulidae*, 2 – *Nectariniidae*, 3 – *Corvidae*, 4 – *Emberizidae*, 5 – *Muscicapidae*, 6 – *Fringillidae*

Group	1	2	3	4	5	6
Av. residual	<u>-0.043</u>	<u>-0.029</u>	<u>-0.006</u>	<u>-0.004</u>	<u>0.016</u>	0.042

A. Taxonomic families within environmental strategy groups: 1 – *Parulidae*, 2 – *Nectariniidae*, 3 – *Corvidae*, 4 – *Emberizidae*, 5 – *Muscicapidae*, 6 – *Fringillidae*

Group	1	2	3	4	5	6
Av. residual	<u>-0.051</u>	<u>-0.048</u>	<u>-0.019</u>	<u>-0.007</u>	<u>0.008</u>	0.077

B. Food strategy groups within taxonomic families: 1 – “nectarivorous”, 2 – “omnivorous”, 3 – “insectivorous”, 4 – “granivorous”

Group	1	2	3	4
Av. residual	<u>-0.047</u>	<u>-0.028</u>	<u>-0.006</u>	0.037

C. Environmental strategy groups within taxonomic families: 1 – “tropical”, 2 – “terrestrial”, 3 – “boreal”

Group	1	2	3
Av. residual	-0.045	<u>0.007</u>	<u>0.021</u>

that only few values diverge from the regression line. On the contrary, in *Nectariniidae* and the groups with many species from this family many values departing from the regression line show that in those groups the effect of body size is smaller and explain a minor part of the total variation in BMR.

Selection of life history traits determines division into strategies. Analysing the segregation of species into groups, based on different assortment of variables (see Appendix), we see that the different classifications do not diverge much from each other. Each of the life history traits used in such a comparative study presumably shows differences in arranging the objects studied, and the less correlated are variables the greater are differences. Thus, the more different traits, including all the periods and stages of life we take into account, the better discernible will be the dependence between them. Then it should be easier to find out which dependence is reflected in energetic costs. The problem does not resolve itself to a number of traits used. A method applied to describe differentiation of the variables is important as well.

When the food variables are examined, the partition into strategies is based on connexions of each species with three factors (Table 1A). Factor 1 combines feeding on various refuses and vertebrates, and less so on green parts of plants. Factor 2 represents a negative correlation between feeding on insects and feeding on seeds. Factor 3 sorts species out according

to soft plant diet. Feeding on nectar is negatively correlated with feeding on fruits and green parts. Among "omnivorous" are the species feeding on the least selected food. The strategies "nectarivorous", "insectivorous" and "granivorous" are based on more selected food. Most of "granivorous" species complete their diet on quite a large scale with various sorts of vegetable food and insects, and "insectivorous", with vegetable food. But "nectarivorous" are specialised in deriving nectar, one of the most specific vegetable foods. The lowest average value of residuals for metabolism in this group (Table 5C) seems to indicate that apart from food habits other factors may influence functional relationships reflected in energetic costs. Analysing the effect of diet on BMR in birds, McNab also noticed that species feeding on insects and their larvae may have both low (*Parulidae*, *Tyrannidae*, *Sylviinae*) and high BMR (*Troglodytidae*, *Paridae*). Thus, the next step was to look for another functional relationships connected with energetic costs alternative to the conclusion of Bennett, Harvey (1987), who consider taxonomic affiliation, beside body size, to be the main source of variation in BMR in birds. The methods they propose seem to be necessary in comparative studies dealing with the arbitrary course of evolution. However, the aim of this work was to check the sources of variability in BMR reflecting the average costs and others which result from various scope, and not from traits inherited by chance, controlled by natural selection after all.

When the relationships between climate, habitat, biotope and nest are considered, one should remember that the division into strategies was based on two factors (Table 1B). The first one, combining biotope, habitat and type of nest seems to reflect adaptations, which order the species according to the way they avoid predators and adverse environmental factors. The second, a combination of climate and type of nest, is most likely connected with breeding season and reproduction.

The group of "tropical" is composed of species living in both wet and dry, tropical climate, generally feeding in tree-tops, often on the wing, building enclosed and woven nests or breeding in holes and other natural shelters. The low metabolic rates of tropical species, compared with species from higher latitudes have already been evidenced (Weathers, 1979; Ellis, 1981; Hails, 1983). It is easy to notice that the species from this group feed generally in a zone of high insolation. The metabolic rate in tropical birds can also be connected with colour of plumage and habitat; dark-plumaged species and those feeding in open sunny places have lower metabolic rate than light-plumaged and feeding in the shade (Weathers, 1979; Ellis, 1981; Hails, 1983). It is confirmable in the "tropical" group although the variable describing colour of plumage has not been used. Breeding in holes and building either enclosed or woven nests suggest another dependence. It may clearly abate the pressure of predators (one should remember that the reproductive time in tropical zone can be very long) which is reflected in energetic costs. Thus, we may suppose that demographic traits connected with reproduction participate in energetic costs. This supposition should be tested using more traits, e.g. life length, brood size, number of hatches in the year, length of the period of hatching, length of the period of feeding or age of maturity.

The higher metabolic rate of "terrestrial" and "boreal" strategists compared to "tropical" probably has other causes. As far as food is concerned the "terrestrial" include species which use the least digestible food, although this trait was not examined directly (habitat

partly determines what is eaten). Thus, the high metabolism may be related to either the extra metabolic costs of digestion and the contribution of symbiotic intestinal flora to the overall metabolic rate, or to the greater pressure of predators in open areas. It demands keeping the body in permanent readiness to escape. Both these effects may be reflected in the BMR. However, the presence of corvids in this group, which have few natural enemies, does not corroborate this hypothesis.

On the other hand, the "boreal" strategists include species from higher latitudes, living in forests or bushes, feeding among vegetation, often near ground (Appendix). Although the basal metabolic rate is from definition without costs of thermoregulation, there are some evidences that in animals living at high latitudes with cold climate and great seasonal changes in temperature the maintenance of constant body temperature is reflected in the BMR (Haim, 1987). Thus, the highest metabolic rate of "boreal" can be linked with costs of thermoregulation, but presumably not only. These birds feed in the most active way. In such a strategy the natural selection should promote evolution of the nervous system, improvement and development of sensory organs and those, which make finding high-value food easier. Therefore, the higher metabolic rate may be related to extra costs of having a large brain, or muscles, or both. The hypothesis is testable, e.g. by morphometric analysis of particular organs and then a comparison between them.

Cluster analysis made for all the variables is based on three factors (Table 2C). Factor 1 combines taking different kinds of food: refuses, vertebrates and green parts of plants, feeding in lower parts of vegetation or on the ground, living in open biotope and living rather as a resident. Factor 2 combines eating nectar, living in warm climate, building enclosed or woven nest, feeding in the canopy layer and living as a resident. The remaining types of plant food (green parts, fruits and seeds) are negatively correlated with these variables. Factor 3 indicates some relationships between eating invertebrates, living in wet biotopes, feeding among vegetation, building better hidden nests and tendency to migrating, contrary to granivorous species.

Group 1 includes food opportunists, often feeding on the ground, and all of them but one species eat seeds. The species from group 2 eat preferably animal food found among vegetation. Most species from group 3 are nectarivorous and preferably feed in tree tops. The species from groups 1 and 2 breed in cooler zones than the species from group 3, but the first group includes resident or nomadic species whereas in the second almost each of them are regular vagrants. Group 3 includes residents, which also build closed nests. This strategy seems to be more different from the others (Fig. 2). Most of residuals for the species from this group are situated below the regression line. This indicates generally lower BMR, especially compared to group 1. Because the third group contains all "tropical" strategists, the characterisation and interpretation may also be similar.

The division into strategies, commanded by food habits, demands a comment. The greater number of food-variables (7) compared to the others (5) probably obscures any relationships between the traits. The problem is that qualitative traits are difficult to categorize. It is not always possible to describe all the traits using identical methods in order to treat them as quantitative traits. The type of food eaten is here a good example and in that case interpretation of the results needs caution.

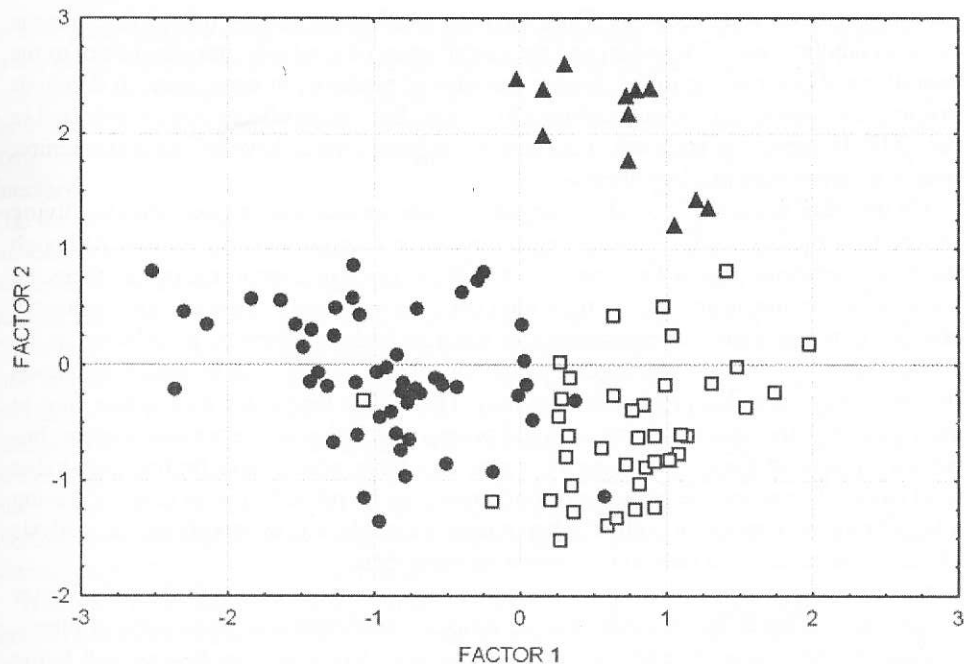


Fig. 2. The scores of Factor 1 and Factor 2 plotted for 122 species of passerine birds. Symbols correspond to strategies: ● = Group 1, □ = Group 2, ▲ = Group 3.

In our interpretation of the variance in BMR we stressed the possible functional significance of higher or lower metabolic rates, as some sets of adaptations are energy-demanding and others may allow for living at a low energy input (Szarski, 1983; Gnaiger, 1987). These “wasteful” and “frugal” adaptations may affect the level of basal metabolism. We also tried to check how the assortment of the life history traits might help to explain the residual variation. The results indicate that differences in ecological factors and diet may affect the basal metabolic rate in passerine birds. The absence of significance when considering strategies based on all variables within the taxonomic affiliation ($p > 0.05$) may suggest that taxonomy explains the greater part of the total variation in metabolism. On the one hand, this observation confirms suggestions of Bennett, Harvey (1987). On the other hand, the probability of obtaining the wider gradient of a trait increases with a number of variables. This may exert an influence on the results (six families to three strategies). Because empirically based allometric relationships are critically dependent on the underlying assumptions of the statistical models, the problem about how far the functional dependences between ecological factors are independent of taxonomic affiliation and whether probabilities do not result from having a common ancestor demand further corroboration by experimental data and alternative models and techniques for analyses.

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No.	Species	Mass [g]	BMR [kJ/d]	Ref.	Life style													Group		
					A	B	C	D	E	F	G	H	I	K	L	M	P	R	W	
108	<i>Pyrrhonorax graculus</i> <i>Parulidae</i> :	191.5	139.01	6, 11	1	1	1	0	1	2	1	2	1	1	2	1	O	Te	1	
109	<i>Dendroica caerulescens</i>	9.4	15.91	1	0	1	0	0	0	2	0	3	4	4	1	5	1	Bo	2	
110	<i>Dendroica coronata</i>	11.5	16.31	9	0	2	1	0	0	2	0	2	3	5	1	4	1	Bo	2	
111	<i>Dendroica dominica</i>	9.8	13.90	9	0	0	0	0	0	3	0	4	3	5	1	2	1	Tr	2	
112	<i>Dendroica palmarum</i>	9.8	13.47	9	0	1	1	0	0	2	0	1	3	2	2	5	1	Bo	2	
113	<i>Dendroica pinus</i>	12.0	15.63	9	0	1	1	0	0	2	0	4	3	4	1	2	1	Tr	2	
114	<i>Geothlypis trichas</i>	10.6	14.88	9	0	1	1	0	0	2	0	3	3	3	1	4	1	Bo	2	
115	<i>Mniotilta varia</i>	8.2	10.92	9	0	0	0	0	0	3	0	3	3	5	2	4	1	Tr	2	
116	<i>Parula americana</i>	7.0	10.64	9	0	1	1	0	0	2	0	3	3	4	3	5	1	Tr	2	
117	<i>Protonotaria citrea</i>	12.8	17.10	9	0	0	0	0	0	3	0	3	2	5	4	5	1	Tr	2	
118	<i>Seiurus aurocapillus</i>	19.0	20.81	9	1	1	1	0	0	2	0	3	1	4	1	5	1	Te	2	
119	<i>Seiurus noveboracensis</i>	18.7	24.09	9	0	1	1	0	0	2	0	1	1	5	4	5	1	Bo	2	
120	<i>Vermivora celata</i>	9.3	12.83	9	0	1	0	0	0	2	0	1	3	5	1	4	1	Bo	2	
121	<i>Vermivora pinus</i>	7.8	13.06	9	0	0	0	0	0	3	0	3	3	3	1	5	1	Bo	2	
122	<i>Wilsonia citrina</i>	12.0	18.58	9	0	1	0	0	0	2	0	3	3	4	1	5	1	Bo	2	

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Cierlik G., Tworek S., Makomaska-Juchiewicz M., Profus P.: **Metabolické hodnoty u spevavých vtákov: vplyvy adaptívnej stratégie a taxonómia.**

V práci sa zaoberáme testovaním hypotézy, že metabolické hodnoty u vtákov sú konvergentné a závisia od funkčnej adaptácie. Testovali sme ako alternatívu, či taxonomické pričlenenie dostatočne objasňuje variáciu v metabolizme. Bazálne metabolické hodnoty (BMH) u 122 druhov zo šiestich čeľadí (*Corvidae*, *Emberizidae*, *Fringillidae*, *Muscicapidae*, *Nectariniidae* a *Parulidae*) spevavých vtákov sme prevzali z literatúry a porovnali s údajmi stravovacích zvykov, klímy, stanovišťa, biotopu, typu hniezda a migrácií. Pomocou faktorovej analýzy a rôznych stratégií klastrovacích procesov sme rozlíšili rôzne kategórie potravy (nektarožravci, hmyzožravci, zrnožravci, všežravci), environmentálne stratégie (terestriálne, tropické, boreálne) a stratégie založené na analýze potravy a zvyšných charakteristík ako „1. skupina“, „2. skupina“, „3. skupina“. Tieto skupiny sa iba čiastočne stotožňujú s taxonomickou klasifikáciou. Všetky skupiny demonštrujú podobnú závislosť BMH od telesnej hmotnosti, ale zrnožravci majú významne vyššiu BMH ako nektarožravci a tropické majú nižšie BMH ako terestriálne a boreálne. Opačne, *Fringillidae* majú významne vyššie BMH ako *Muscicapidae*, *Emberizidae*, *Nectariniidae* a *Parulidae*. Analýza reziduí v rámci ANCOVA naznačuje, že taxonomické pričlenenie má väčší vplyv na hodnoty BMH ako adaptívna stratégia.