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CLUSTER-BASED APPROACH FOR IDENTIFYING AVIAN LIFE-HISTORY GROUPS FOR USE IN ECOLOGICAL MONITORING

ABSTRACT: Almost 'since ever' ecologists have made attempts at the generalization of various site-specific, species-specific and time-specific situations, including different classifications of species, based on different principles and prepared for different purposes. This paper, presenting a conceptual model for selecting species of similar life-history pattern to other species and providing an example using birds as a model system, represents that current in the ecology. All bird species regarded as nesting in a given area of the mosaic landscape in southern Poland were described with respect to nine variables (nest type, nest location, food habits, place and way of foraging, migration status, number of broods, clutch size, incubation and fledging periods), grouped into 43 categories. Cluster analysis was then used to distinguish objectively species displaying similar life history traits and environmental adaptations into unique life-history 'strategies'. The results of an exemplary analysis of variability in the density, domination, number of species and turnover rate in particular strategies, depending on the size of study plots, their structure, degree of isolation and the characteristic features of their surroundings, using regression and canonical correlation techniques, indicate the suitability of this approach to testing detailed hypotheses connected e.g. with studies on the response of species to different habitat conditions. The methods applied allow one to distinguish, in an objective way, the groups of species displaying similarities with respect to life history traits and environmental adaptations, in spite of the fact that the method of describing variables in cluster analysis may determine a different allocation of species to groups. A model, as described, could allow conservation principles to be developed for species of similar distribution, ecological feature or life history; especially for those species which face with population declines and for which no previous patterns have been established.

KEY WORDS: bird species, cluster analysis, ecological features, grouping criteria, life histories, life strategies

1. INTRODUCTION

Birds are good indicator species because this group of animals is probably better investigated and monitored than any other groups of animals or plants (Tucker and Heath 1994). By combining species into categories that reflect selected traits, previous investigators have examined the change in avifauna associated with changing environmental conditions. Even when the group of avian species was distinguished, studies differ with respect to the objectives and methods used and, thus, grouping criteria varies. For example, groups of species can be arrayed on the basis of foraging techniques (Cotgreave and Harvey 1992), propensity to migrate (Böhning-Gaese and Bauer 1996), or habitat occupied (Jokimäki and Huhta 1996, Germaine *et al.* 1997). Bentley and Catterall (1997) applied several other criteria by comparing the taxonomic families and 'functional groups' based upon foraging technique and diet, reaction to reduced resources availability and migration strategy. In studies of the phenomena mentioned above, ecologists often rely on 'guilds' and 'functional groups' as their basic unit of observation, sometimes treated as a starting point to test more detailed hypotheses (Wiens 1989). The division into guilds is made most often on the basis of food resources and foraging (Miller and Cale 2000, Lindsay *et al.* 2002), habitat preferences (Jansson 1998, Whitaker and Montevecchi 1999) or migrating and nesting habits (Kropil 1996, Hobson and Bayne 2000). Unfortunately, the method by which species are classified into guilds is often unclear, nor how the method used to classify guilds is related to the concept being studied (Wilson 1999).

All the classifications discussed above attempt to distinguish species with respect to a predefined factor, after which an attempt is made to investigate group similarities and differences in response to said factor. Another approach leads to group the species basing on the response of species to a studied factor. Some researchers, having adopted this approach, e.g. in the analysis of the relationship between the occurrence of birds and the structure of vegetation in fragmented woods or from the characteristics of habitats, formulate conclusions pertaining to groups of species responding likewise (Bersier and Meyer 1994, Petersen 1998). I used a similar way of drawing conclusions in the studies of breeding bird assemblages in an agricultural landscape in southern Poland (Tworek 2002), where I tested the responses of birds to habitat changes. This paper represents an attempt to verify the methods used in the solution applied in the previous paper (i.e. arraying groups on the basis of many characteristics considered at once). Recent methodological advances to differentiate objectively the species partition into guilds and functional groups provide the means to construct an operational framework for making experiments that are urgently needed for a better understanding of the role of species in ecosystem functioning (Blondel 2003). The aim of this study is to analyze the methodological solutions applied in the investigation of the response of birds to environmental changes with a focus on the advantages and disadvantages of the approach combining many classification criteria. As one of the ways to find indicator species and identify their responses to given habitat changes, such a model can be a starting point to test hypotheses and find applications in landscape ecology, conservation biology and land-use management. The possibility of interpretation of the results gives certain indications of the suitability of the model in ecological studies. It also provides a material for discussion of the advantages and disadvantages of the approach used.

2. METHODS

The model is based on methods described in the paper by Tworek (2002). This paper focuses on the issues omitted in the previous paper which are necessary to present a theoretical framework for the model. The field studies that provided the initial material were conducted from 1995 to 1998, but the testing used the results of one more year of study (1999). Using the territory mapping method (Bibby *et al.* 1992), I estimated the population of nesting birds on 38 habitat islands, in the context of highly fragmented landscape in Małopolska (southern Poland; 50°06′–50°08′ N, 19°45′–19°55′ E, *ca.* 44 km^2). All the bird species regarded as nesting in the study area were described with respect to their characteristics and preferences towards nine species-specific variables. The variables considered were as follows: nest type, position of the nest, type of food taken, location and method of foraging, type of migration, number of broods in a year, clutch size, duration of incubation, and the time lapsing between hatching and fledging. Each of the variables was described in the gradient (from three to six categories) differentiating the feature referred to, depending on the range of variation of particular variables in the studied assemblages of breeding birds (Table 1). Next, using predominantly published information (Bauer and Berthold 1997, Glutz von Blotzheim and Bauer 1980, Cramp 1988, Hagemeijer and Blair 1997, Snow and Perrins 1998), sometimes augmented by my own field observations, I described particular species in a binary system, ascribing either a "1" or "0" symbol to each of the categories of variables, depending on whether they pertained to the species or not. The categories differentiated within a given variable were not necessarily mutually exclusive (i.e. within each variable there could be more than one category given a value of 1). Therefore each species was described by a binary code (the total of 43 categories of variables), which defined its ecological preferences and adaptive traits (Tworek 2002).

Using the life-history data I completed a cluster analysis in order to select groups of species of similar lifestyles. Each species was treated in this analysis as an independent data point (see Harvey and Pagel 1991). Using Ward's method in joining analysis (StatSoft Inc. 1997), I checked the lack of homogeneity of the entire dataset described according to the categories. After the analysis of linkage distances on a tree diagram, I formulated the hypothesis based upon the number of clusters that would order the species in a way that reflected their different life-histories and represented the differences in ways in which these avian species respond to habitat changes. I conducted k-means clustering, maximizing the distances between clusters when calculating initial cluster centers. The general logic of the method consists in distinguishing groups, in this case bird species, which will display the greatest differences possible: in the division into these groups, the variability within clusters is minimised whereas the variability between clusters is maximised. It is a kind of 'ANOVA in reverse', because for the hypothesis stating that the means in the groups differ from each other, the test of significance in ANOVA evaluates the between-group variability against the within-group variability. The procedure of grouping in the k-means method, tries to transfer objects (bird species) to and from groups (clusters) to obtain the most significant ANOVA results. Having analyzed the means for each cluster in each dimension (Table 1), I made the initial characterization of 'clusters'. For the sake of simplicity, I treated the groups of species so distinguished as strategies.

Next, using models of stepwise multiple regression, I analyzed the variability of population densities, domination, number of species displaying particular strategies, and their turnover rate depending from the size, shape and perimeter of study plots, density of various layers of vegetation, the variability in habitat structure, isolation and the features of surroundings. Comparing the results obtained for particular strategies I checked whether their responses to habitat changes were different. Canonical correlation analysis was used to generalise the results of the multiple regression analyses and to evaluate a relationship between the bird strategies and the environment.

3. RESULTS AND DISCUSSION

3.1. Groups of species and life strategies

The characteristics of each strategy in relation to the nine initial variables are shown (Table 1). It should be noted that this kind of brief summary does not illustrate equally well the traits of each species within a given strategy. For attempts of this kind it is unavoidable and the more difficult the interpretation of a classification, the more 'imperfect' will probably be the selection of variables. In such a case, the search for more variables, potentially capable of significant effects on the results and their interpretation, should continue. As the objective of this work is not to fit optimally the variables in the model but to follow a mechanism, it is enough to remember that the adopted classification is only a kind of approximation (i.e. other classifications are also possible and liable to interpretation).

Table 1. Categories of variables describing bird species and their average values (± SD) for strategies I–V (see the text). Value "0" means that a variable does not refer to any species of a given strategy; value "1" means that a variable refers to all the species of a given strategy. For each category F-ratio from k-means cluster analysis is placed.

Variables and their categories	Strategies					F ratio
	I	II	III	IV	V	
Nest type						
1. Nest open uncovered	0.58 (0.51)	0.80 (0.41)	0	0.54 (0.51)	0.75 (0.44)	15.7
2. Nest open covered or semi-open	0.83 (0.39)	0.10 (0.31)	0.34 (0.48)	0.86 (0.36)	0.55 (0.51)	8.3
3. Nest enclosed	0	0.05 (0.22)	0.07 (0.26)	0.14 (0.36)	0.15 (0.37)	1.2
4. Nest hidden	0	0.20 (0.41)	0.90 (0.31)	0.04 (0.19)	0.05 (0.22)	54.3
Nest location						
1. Nest on the ground	0.83 (0.39)	0.10 (0.31)	0	0.61 (0.50)	0.15 (0.37)	7.6
2. Nest in vegetation up to 1.5 m high	0.08 (0.29)	0	0	0.64 (0.49)	0.40 (0.50)	11.6
3. Nest in a hole or den	0	0.10 (0.31)	0.86 (0.35)	0.07 (0.26)	0.05 (0.22)	49.4
4. Nest on trees or shrubs above 1.5 m high	0.08 (0.29)	0.75 (0.44)	0.03 (0.18)	0.21 (0.42)	0.85 (0.37)	16.5
5. Nest at the water	0.33 (0.41)	0.20 (0.41)	0.07 (0.26)	0.11 (0.31)	0	3.4
6. Nest on anthropogenic elements	0	0.20 (0.41)	0.28 (0.45)	0.11 (0.31)	0.10 (0.31)	0.7
Place and way of foraging						
1. Foraging in water	0.33 (0.49)	0.20 (0.41)	0	0.07 (0.26)	0	5.1
2. Foraging on the ground	1	0.90 (0.31)	0.41 (0.50)	0.54 (0.51)	0.70 (0.47)	4.7
3. Foraging in the undergrowth zone	0	0.20 (0.41)	0.10 (0.31)	0.75 (0.44)	0.70 (0.47)	17.1
4. Foraging in the trunk and branches zone	0	0.55 (0.51)	0.79 (0.41)	0.14 (0.36)	0.40 (0.50)	10.3
5. Foraging in the canopy zone	0	0.25 (0.44)	0.52 (0.51)	0.57 (0.50)	0.85 (0.37)	12.9
6. Foraging actively in flight	0	0.55 (0.51)	0.31 (0.47)	0.43 (0.50)	0.10 (0.31)	6.8
Migration status						
1. Feeding on green parts of plants	0.75 (0.45)	0.20 (0.41)	0.07 (0.26)	0.04 (0.19)	0.30 (0.47)	23.5
2. Feeding on fruits	0.75 (0.45)	0.35 (0.49)	0.17 (0.38)	0.29 (0.46)	0.60 (0.50)	11.6
3. Feeding on seeds	0.75 (0.45)	0.30 (0.47)	0.10 (0.31)	0.04 (0.19)	0.65 (0.49)	27.0
4. Feeding on invertebrates (other than insects)	0.92 (0.29)	0.55 (0.51)	0.10 (0.31)	0.46 (0.51)	0.30 (0.47)	8.7
5. Feeding on insects	0.92 (0.29)	0.80 (0.41)	0.97 (0.18)	1	0.70 (0.47)	5.1

Variables and their categories	Strategies					F ratio
	I	II	III	IV	V	
6. Feeding on vertebrates Migration status	0	1	0.03 (0.18)	0.04 (0.19)	0	25.3
Food habits						
1. Sedentary species	0.17 (0.39)	0.65 (0.49)	0.52 (0.51)	0	0.45 (0.51)	6.9
2. Nomadic species or short-distance migrant	0.08 (0.29)	0.50 (0.51)	0.14 (0.35)	0	0.65 (0.49)	7.7
3. Average-distance (European) migrant	0.67 (0.49)	0.20 (0.41)	0.14 (0.35)	0.21 (0.42)	0.55 (0.51)	4.2
4. Tropical migrant	0.25 (0.45)	0.20 (0.41)	0.31 (0.47)	0.79 (0.42)	0.05 (0.22)	20.1
Number of broods per year						
1. One brood	0.75 (0.45)	1	0.76 (0.43)	0.75 (0.44)	0.15 (0.37)	13.0
2. Two broods	0.25 (0.45)	0.10 (0.31)	0.59 (0.50)	0.57 (0.50)	0.90 (0.31)	7.6
3. Three or more broods	0.17 (0.39)	0	0.07 (0.26)	0.04 (0.19)	0.50 (0.51)	5.4
Clutch size						
1. 1–2 eggs	0.08 (0.29)	0.35 (0.49)	0.07 (0.26)	0.04 (0.19)	0.15 (0.37)	6.1
2. 3–5 eggs	0.42 (0.51)	1	0.55 (0.51)	1	0.70 (0.47)	9.1
3. 6–8 eggs	0.08 (0.29)	0.50 (0.51)	0.90 (0.31)	0.64 (0.49)	0.35 (0.49)	7.3
4. at least 9 eggs	0.58 (0.51)	0	0.28 (0.45)	0.04 (0.19)	0.10 (0.31)	6.5
Incubation period						
1. to 12 days	0.08 (0.29)	0	0.48 (0.51)	0.79 (0.42)	0.75 (0.44)	16.6
2. 13–16 days	0	0.05 (0.22)	0.90 (0.31)	0.75 (0.44)	1	49.9
3. 17–21 days	0.50 (0.52)	0.40 (0.50)	0.21 (0.41)	0.07 (0.26)	0.20 (0.41)	9.7
4. 22–29 days	0.67 (0.49)	0.40 (0.50)	0	0	0	21.3
5. at least 30 days	0	0.50 (0.51)	0	0	0	44.3
Fledging period						
1. to 12 days	0.08 (0.29)	0	0.03 (0.18)	0.75 (0.44)	0.45 (0.51)	16.1
2. 13–16 days	0.25 (0.45)	0.05 (0.22)	0.28 (0.45)	0.68 (0.48)	0.75 (0.44)	10.9
3. 17–22 days	0.42 (0.51)	0.15 (0.37)	0.72 (0.45)	0.18 (0.39)	0.55 (0.51)	9.4
4. 23–30 days	0.17 (0.39)	0.45 (0.51)	0.41 (0.50)	0	0.05 (0.22)	6.3
5. longer than 30 days	0.50 (0.52)	0.80 (0.41)	0.03 (0.18)	0	0.05 (0.22)	57.1

Strategy I

The species of open spaces, the least associated with woods, were allocated to strategy I. They stand out among all groups for they have the highest proportion of plant forage in their diet. Nevertheless, members of this group prefer to feed on insects and other invertebrates. Their nests are open and placed on the ground. These species are most commonly European migrants and compared with species classified into other strategies they have the largest size of brood of eggs. The most numerous species of the "open space" group were (in descending order): Eurasian Sky Lark *Alauda arvensis*, Lapwing *Vanellus vanellus*, Mallard *Anas platyrhynchos*, Corncrake *Crex crex* and Grey Partridge *Perdix perdix*.

Strategy II

The species allocated to strategy II are predators. All feed upon vertebrates, to a variable degree. Like the previous group, these species also have open nests but, in this case, place them high above ground. Species in this group are mostly resident, have a single brood with a small number of eggs, and have the longest incubation and fledging periods relative to other groups. In this group the most numerous species were: Magpie *Pica pica*, Eurasian Kestrel *Falco tinnunculus*, Carrion Crow *Corvus corone*, Jay *Garrulus glandarius* and Buzzard *Buteo buteo*.

Strategy III

The species allocated to strategy III have their nests in tree hollows or otherwise are hidden. Species in this group feed among trees and shrubs (between trunks and boughs), often actively in flight, they feed chiefly on insects, are either resident or migrating over long distances. Species belonging to this strategy include among others the Great Tit *Parus major*, Starling *Sturnus vulgaris*, Blue Tit *Parus caeruleus* and Tree Sparrow *Passer montanus*.

Strategy IV

The species of strategy IV place their nests low above ground, they are insectivorous and feed most often in the herbaceous and undergrowth layer, often in flight. Members of this strategy are Tropical migrants, having the shortest incubation and fledging times among all groups. The species of this group were the most common in the study, including the Marsh Warbler *Acrocephalus palustris*, Whitethroat *Sylvia communis*, Whinchat *Saxicola rubetra* and Willow Warbler *Phylloscopus trochilus*.

Strategy V

Finally, the species of strategy V build their nests in trees and bushes, and avoid wetlands and areas near bodies of water. Members of this group are mostly short-distance migrants and have the highest number of broods in a year among all the groups (Table 2). Because species in this strategy are mostly herbivorous, the proportion of insectivorous species is the lowest when compared with the other strategies. In this group the most numerous species were: Chaffinch *Fringilla coelebs*, Fieldfare *Turdus pilaris*, Goldfinch *Carduelis carduelis*, Yellowhammer *Emberiza citrinella*, Blackbird *Turdus merula*, Reed Bunting *Emberiza schoeniclus*, Linnet *Carduelis cannabina* and Woodpigeon *Columba palumbus*.

The above classification differs from the division into guilds, frequently applied by ornithologists (Jansson 1998, Hobson and Bayne 2000, Miller and Cale 2000), in that the strategies have been distinguished on the basis of many traits. Guilds most often concern single traits and then attributing a given trait to a species may be subjective. Cluster analysis, based on many traits, described in detail as in the presented model, minimizes this subjectivism.

The results of stepwise multiple regression and canonical correlation analyses obtained in the above mentioned study (Tworek 2002), clearly show that groups of species can either respond positively or negatively to different habitat changes within a fragmented landscape. Depending upon the strategy, variability of the studied parameters can be explained by interrelationships between occurrence of open and tree-covered habitats, degree of landscape

Table 2. Characteristics of life strategies I–V (see the text) in relation to 9 species-specific variables.

Variables	Strategies				
	I	II	III	IV	V
Nest type	open, often covered	mostly open uncovered	never open uncovered, often hidden in a hole	open covered or semi-open, sometimes enclosed	mostly open uncovered, more seldom open covered or enclosed
Nest location	on the ground, often at water	on trees and shrubs (usually high) or on anthropogenic elements	never on the ground or in vegetation close to the ground, mostly in a hole, den, building etc.	usually in vegetation close to the ground	on trees or shrubs
Food habits	highest proportion of plant food in diet, invertebrates	vertebrates preferred	insects almost exclusively	insects, supplemented by other invertebrates and by fruits	plant and animal food items (except vertebrates) equally preferred
Place and way of foraging	exclusively on the ground or in water	mostly on the ground (all habitat zones possible), often active search	tree trunk and bough zones, never in water	preferably close to the ground, in undergrowth, more rarely in canopy zone, often active search	most often in canopy zone, and elsewhere except for water
Migration status	most often European migrants	all types of migrations, the highest number of resident species	resident or Tropical migrants	almost exclusively Tropical migrants	wandering species, short-distance migrants
Number of broods	1–3, most often 1 brood	almost always 1 brood	1 or 2 broods	1 or 2 broods	almost always at least 2 broods
Clutch size	3–5 eggs or more than 9	up to 6 eggs, 3–5 on average	at least 5 eggs, most often 6–8	usually 5–8 eggs	most often 3–5 eggs
Incubation period	usually 17–25 days	at least 20 days	most often 13–16 days	up to 16 days, less than 13 days in most of species	13–16 days
Fledging period	variable, usually more than 16 days, precocial species included here	usually at least 30 days	most often 17–22 days	up to 14 days	most often 13–18 days

patchiness, presence of mature tree stands and/or degree of habitat humidity and vegetation structure. Generally, the negative consequences of habitat changes affect the forest interior species and species living in open wet biotopes. On the other hand, the same changes can increase the attractiveness of an area for quickly adapting species. Attempts to identify and interpret the importance of different habitat factors, in determining the occurrence of breeding birds, revealed that responses differ depending on the overall strategy of the species based on both demographic characteristics and adaptations to environmental factors.

3.2. How to distinguish strategies: verification of the method

Multidimensional statistical methods provide for the possibility of using different algorithms for grouping. In the described model I applied k-means cluster analysis to differentiate strategies among birds. Despite there are some ways of determining the number of clusters that are statistically meaningful (Anderson and Clements 2000), the inconvenience of this method lies in the necessity to take eventually a decision about the number of clusters for dividing the objects analyzed. Such an issue does not appear in the case of interval variables where the classification depends principally on the treatment of the variables measured. It may be of significant importance, however, in the case of nominal and/or ordinal variables. For example, from the viewpoint of inclination towards migration, birds may generally be divided into resident and migratory species. Next, the migratory birds may be divided into tropical migrants and European migrants. When needed, this classification may be even more detailed, thus increasing the gradient of variable between the most extreme categories, in this case pertaining to their sedentary and migratory characteristics.

Cluster number is dependent upon the scale at which various variables are measured, something that is determined *a priori* by the researcher, based upon the specific objective of the study. Assigning species to particular classes (in this case functional groups), however, can be problematic. Often, the trait being examined may not be known or it may be phenotypically plastic, such that assignment proves difficult. For example, should Linnet or Reed Bunting be classified as resident species or as migrating ones? Even when we consider the fact that the level of migratory tendency varies within a continent (e.g. a species that is migratory in Scandinavia may be resident in the Mediterranean), some species actually exhibit differences within a country. Other classifications based upon diet can prove challenging when species are labeled insectivorous when some members may actually be omnivorous (e.g. skylarks) or when granivorous birds switch their diet during the breeding season to an insectivorous one (e.g. Yellowhammer).

With all the inherent problems associated with assigning species to functional groups, many authors have used specific data from literature (Cieślak 1994, Elmberg and Edenius 1999, Jokimäki 1999, Clergeau *et al.* 2001), sometimes supplementing them with their own observations from their respective study areas. The method applied in the present model shows that problems may be avoided by using unambiguous (i.e. simple, easy to differentiate, and based on clear-cut criteria) categories of variables. As such, the risk of misclassifying species to an incorrect category is minimized and, thus, reducing the introduction of false information. Of course, information is lost when, for example, an omnivore is assigned to a specific diet type (e.g. insects, grains or fruits). The investigator must weigh the costs of being too specific with categorical variables against being too general.

The aforementioned inconvenience of the k-means clustering lies in the necessity to decide about the number of clusters to allocate the cases or variables. Immediately a question arises, why it is just dividing into five groups that best reflects the differences in life strategies of birds in the study area? In order to find it, one might check all possible allocations of species, starting from two groups. The statistical packages available will "deal" very quickly with such a task. But more problems lie ahead when it comes to analyzing the results of allocation and interpretation thereof. A scientist should nevertheless have a remarkably stronger argument to either confirm or reject his intuition presented in form of hypotheses. In order to acquire such an argument, prior to an analysis of the grouping by the k-means method, I had grouped the species using tree clustering.

The tree clustering method uses the dissimilarities or distances between objects when forming the clusters. These may be distances in one dimension or multiple dimensions. The most straightforward way of computing distances between objects in a multidimensional space which I utilized also in this paper, is by calculating the Euclidean distances. If we consider two- or three-dimensional space, this measure is the actual geometric distance between objects. From the viewpoint of the logic of an algorithm, of joining it is just the same, whether the distances given are actual distances or any other derived measures of distance which are more important to the researcher; since the choice of suitable measure is his. In the further course of joining we need a principle of linking which will indicate when two clusters are similar enough to allow combining them. The Ward's method used for this end utilizes the variance analysis approach, aiming at minimization of the sum of squares of any two (hypothetical) clusters which may be formed at each step. According to simulation studies by Grabiński and Sokołowski (1980), it is the most effective method in detecting the true structure of data. Another advantage of the method is that it allows verification of the hypothesis of homogeneity of the whole set of data (i.e. it answers the question as to whether the collection of objects, in this study – bird species – should be divided at all). This removes the need to take subjective decisions because the method determines the kind of classification that may reflect the differences among species vis-à-vis the analyzed variables (Fig. 1).

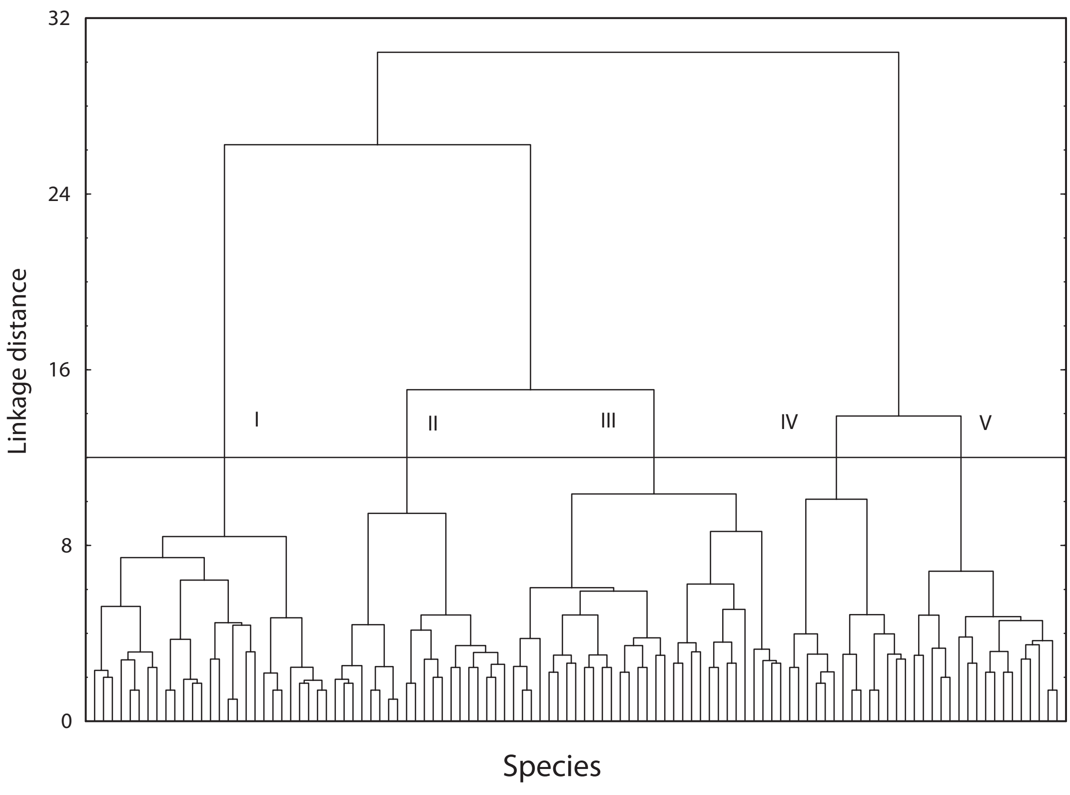

Fig. 1. Joining of species according to Ward's method. Horizontal line cuts species into five groups (life strategies I–V, see the text). This analysis was helpful in taking the decision into how many groups divide the set of studied species.

In analyzing more detailed hypotheses (e.g. looking for linkages between the strategies used by bird species and their ways of responding to habitat changes), the variables provide the basis for dividing species in cluster analysis. Each of the traits used in such comparative studies will show certain variability in ordering the studied objects, and the differences will be greater in line with the weakening of the correlation between the traits studied. Our intuition might suggest that the more traits and the more differentiated ones, covering all periods and phases of birds' lives we consider, the more effective will be the understanding of the relationships between them. In consequence, we should be able to discover which kinds of relationships are reflected, for instance, in the distribution of birds in a landscape with diverse habitats. This problem is not limited only to the number of traits analyzed. As it was shown above, the method of describing the differentiation of variables might be equally important for the final conclusions. Taking into account that each trait consists of 3–6 categories, the ultimate classification was done on the basis of 43 variables describing the life strategy of birds. It may be supposed that with this number of dimensions, the results of cluster analysis should be objective to a great extent. The formula of maximising distances between clusters which I used for choosing the initial centres of clusters, leads quite often to the creation of groups from single objects when the data include evident cases differing significantly from the mean (StatSoft Inc. 1997). The strategies so distinguished include between 12 to 28 (average of 20.5) breeding species, which supports that the formula applied is proper.

To wrap up the discussion of the method of forming groups of different life strategies, it is worth noting that the cluster analysis is not a typical statistical test but rather a collection of various algorithms serving the purpose of grouping objects into clusters. The point is that in contrast to many other statistical procedures, the cluster analysis methods are used mostly when we have no *a priori* hypotheses at hand, but we are still in an exploratory stage of research. The determination of life strategies in birds is a good example, because the variables that may be taken into account do not suggest to which group a species will be classified. Even more, it is impossible to decide prior to the analysis, whether or not the bird species described according to categories listed in Table 1, represent a sample generated by a single, multidimensional distribution of probability. If so, it would mean that there is no ground for rejecting the hypothesis of homogeneity. In a way, the cluster analysis provides the most significant possible solution. For this reason, testing statistical significance does not apply even in those cases where *P* levels are given, for example, when grouping by the k-means method.

4. CONCLUSION

Finally, it is worth considering where the suggested model can potentially find application. It is difficult to imagine that, in any near or even further perspective, natural science will be able to attempt detailed studies of each species in each situation (this would often not be advisable not only because of the immense numbers but also the diversity of conditions and related problems), in order to bring into existence a set of fixed scientific premises to be then used in nature conservation and the management of its resources in quite diverse specific conditions, often very complex, which we face in the rapidly changing environment. There is no doubt whatsoever, that more experimental studies are needed for this purpose, but nevertheless the logistical problems in carrying out such experiments at broad spatial scales or with organisms as mobile as birds are often paramount (Robinson *et al.* 1992, Wiens 1994). One of the possible solutions is to find indicator species of different susceptibility to environmental changes depending on the type of ecosystem. Such species could then used as a kind of pattern for applying measures with respect to other species, similar in terms of occurrence, ecological features or life history traits (Collins *et al.* 1993, Wiens *et al.* 1993). In this paper I have suggested a certain methodological approach to the issue of searching for indicator species and to problems relating to practical application of the model. The presented approach was tested on an example of a study, aimed at answering whether similarity in ecological features and life histories is reflected in the distribution of birds and parameters of their occurrence (Tworek 2002). Keeping in mind certain limitations (e.g. that a model for a given strategy may 'fit' best the most numerous species, while not necessarily fitting the rarest species to the same degree) it seems that this kind of approach may find wider application in landscape ecology and nature conservation. Nevertheless, further studies of this issue are advisable to check whether this method would potentially apply to birds in other landscapes as well as to other groups of animals and/or plants.

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APPENDIX

Breeding birds recorded in studied area during 1995–1999 listed according to their life strategies (I–V, see Tables 1, 2 and the text) and percent of species domination within the strategies.

I (n = 12)	%
Corncrake *Crex crex*	5.7
Grey Partridge *Perdix perdix*	5.4
Lapwing *Vanellus vanellus*	13.0
Mallard *Anas platyrhynchos*	7.6
Moorhen *Gallinula chloropus*	0.7
Pheasant *Phasianus colchicus*	18.1
Quail *Coturnix coturnix*	2.1
Redshank *Tringa totanus*	0.5
Eurasian Sky Lark *Alauda arvensis*	45.4
Snipe *Gallinago gallinago*	0.9
Spotted Crake *Porzana porzana*	0.4
Woodcock *Scolopax rusticola*	0.2
II (n = 14)	
Buzzard *Buteo buteo*	5.5
Carrion Crow *Corvus corone*	9.8
Great Grey Shrike *Lanius excubitor*	1.3
Hobby *Falco subbuteo*	2.2
Jay *Garrulus glandarius*	7.1
Eurasian Kestrel *Falco tinnunculus*	11.6
Kingfisher *Alcedo atthis*	1.8
Long-eared Owl *Asio otus*	0.5
Magpie *Pica pica*	52.2
Marsh Harrier *Circus aeruginosus*	0.9
Raven *Corvus corax*	1.3
Sparrowhawk *Accipiter nisus*	0.9
Tawny Owl *Strix aluco*	1.8
White Stork *Ciconia ciconia*	3.1
III (n = 25)	
Black Redstart *Phoenicurus ochruros*	1.9
Black Woodpecker *Dryocopus martius*	0.7
Blue Tit *Parus caeruleus*	14.5
Coal Tit *Parus ater*	2.7
Collared Flycatcher *Ficedula albicollis*	1.3

Great Spotted Woodpecker *Dendrocopos major*	2.4
Great Tit *Parus major*	24.5
Green Woodpecker *Picus viridis*	0.4
Grey-headed Woodpecker *Picus canus*	0.6
Lesser Spotted Woodpecker *Dendrocopos minor*	1.8
Marsh Tit *Parus palustris*	1.1
Middle Spotted Woodpecker *Dendrocopos medius*	0.4
Nuthatch *Sitta europaea*	3.1
Penduline Tit *Remiz pendulinus*	0.7
Pied Flycatcher *Ficedula hypoleuca*	1.6
Redstart *Phoenicurus phoenicurus*	0.6
Short-toed Treecreeper *Certhia brachydactyla*	0.9
Spotted Flycatcher *Muscicapa striata*	2.3
Starling *Sturnus vulgaris*	22.2
Stock Dove *Columba oenas*	0.2
Syrian Woodpecker *Dendrocopos syriacus*	0.6
Treecreeper *Certhia familiaris*	0.9
Tree Sparrow *Passer montanus*	9.8
Willow Tit *Parus montanus*	4.1
Wryneck *Jynx torquilla*	0.7
IV (n = 28)	
Barred Warbler *Sylvia nisoria*	0.4
Blackcap *Sylvia atricapilla*	7.4
Chiffchaff *Phylloscopus collybita*	1.7
Cuckoo *Cuculus canorus*	1.0
Garden Warbler *Sylvia borin*	2.9
Golden Oriole *Oriolus oriolus*	1.5
Grasshopper Warbler *Locustella naevia*	2.0
Icterine Warbler *Hippolais icterina*	3.4
Lesser Whitethroat *Sylvia curruca*	1.0
Marsh Warbler *Acrocephalus palustris*	31.3
Meadow Pipit *Anthus pratensis*	2.0
Nightingale *Luscinia megarhynchos*	2.0
Red-backed Shrike *Lanius collurio*	3.1
Reed Warbler *Acrocephalus scirpaceus*	0.3
River Warbler *Locustella fluviatilis*	1.7
Robin *Erithacus rubecula*	1.7

Scarlet Rosefinch *Carpodacus erythrinus*	0.6
Sedge Warbler *Acrocephalus schoenobaenus*	0.4
Stonechat *Saxicola torquata*	2.4
Thrush Nightingale *Luscinia luscinia*	0.1
Tree Pipit *Anthus trivialis*	0.9
Wheatear *Oenanthe oenanthe*	0.2
Whinchat *Saxicola rubetra*	6.1
White Wagtail *Motacilla alba*	0.7
Whitethroat *Sylvia communis*	14.7
Willow Warbler *Phylloscopus trochilus*	5.3
Wood Warbler *Phylloscopus sibilatrix*	1.0
Yellow Wagtail *Motacilla flava*	4.2
V (n = 19)	
Blackbird *Turdus merula*	7.3
Bullfinch *Pyrrhula pyrrhula*	0.1
Chaffinch *Fringilla coelebs*	15.3
Collared Dove *Streptopelia decaocto*	1.9
Dunnock *Prunella modularis*	0.7
Fieldfare *Turdus pilaris*	11.1
Goldcrest *Regulus regulus*	0.2
Goldfinch *Carduelis carduelis*	12.1
Greenfinch *Carduelis chloris*	4.3
Hawfinch *Coccothraustes coccothraustes*	1.7
House Sparrow *Passer domesticus*	3.0
Linnet *Carduelis cannabina*	9.5
Reed Bunting *Emberiza schoeniclus*	9.9
Serin *Serinus serinus*	2.0
Song Thrush *Turdus philomelos*	1.2
Turtle Dove *Streptopelia turtur*	1.5
Woodpigeon *Columba palumbus*	6.6
Wren *Troglodytes troglodytes*	0.3
Yellowhammer *Emberiza citrinella*	11.3