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Differences in the nestling diets of sympatric Redstarts *Phoenicurus phoenicurus* and Black Redstarts *P. ochruros*: Species-specific preferences or responses to food supply?

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Abstract. We have investigated whether differences in nestling diet found between locally sympatric Redstarts and Black Redstarts are caused by species-specific preferences or by a different food supply in their territories. The diet of nestlings in a mosaic-like urban environment was studied using the neck-collar method. We found no significant difference in the length of Redstart and Black Redstart prey items. However, the two species did bring to their nestlings invertebrates of different taxa. We used the variance partitioning method based on multivariate Redundancy Analysis to test the influence of habitat, timing of breeding, and the species of redstart itself on nestling-diet composition. Most of the variance in the nestling diet (all the canonical axes explained 70.6% of the variance) could be attributed to habitat variables (34%) and the timing of breeding (8.9%), but only 8.1% to the species of redstart. We suggest that the diet of the two redstart species is influenced largely by current prey availability and, consequently, that interspecific competition is avoided primarily by territory exclusion rather than by food-niche separation. We consider the variance partitioning method to be a powerful tool for identifying the effects of various explanatory variables that could influence food composition in birds.

Key words: diet selection, interspecific competition, local sympatry, urban environment, seasonal variation, Redundancy Analysis, variance partitioning

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INTRODUCTION

Identification of mechanisms allowing for the coexistence of sympatric species belongs to central issues of community ecology. The coexisting species are expected to evolve strategies of niche differentiation, which enable them to avoid competition for limited resources in areas of sympatry (Pianka, 1969, Schoener 1974, 1986). Differentiation of food resources is one of the most important modes of resource partitioning in birds (Newton 1998). Reduction of the food-niche overlap may result from differences in the type and size of prey items or from the segregation of foraging areas (Tokeshi 1999). Food composition and quantification of the dietary overlap in the coexisting species was analysed in numerous studies (Nilsson 1984, Chapman & Rosenberg 1991, Bureš 1994, 1995, Rolando & Laiolo 1997, Gerstell & Bednarz 1999, Leme 2001, Dyrcz & Flinks 2003, Garcia & Arroyo 2005). In spite of that, many aspects of field studies of the competition for food between sympatric species remain methodologically problematic. The birds reflect the temporal and spatial variation in prey availability, and the current food supply strongly affects the diet composition (Jaksic & Braker 1983, Recher 1990). Especially in birds feeding on invertebrates, the food supply may vary not only between years and localities, but also within the season and on a finer scale, among the individual territories (Cooper & Whitmore 1990, Wolda 1990). At the same time, the availability of invertebrates is difficult to quantify, especially in those species searching for food in structurally complex habitats (Hutto 1990). In these cases, it is difficult to separate the species-specific food preferences from a response to different food supply.

The coexistence of the Redstart and Black Redstart is a typical case. The two species differ in their habitat requirements, one of them occupying primarily woods (Redstart) and the other open rocky terrains (Black Redstart). However, the two species often come in a close contact in a mosaic urban environment (Kelcey & Rheinwald 2005). We studied the coexistence of redstarts in an urban habitat where they occupied exclusive territories of different habitat compositions and were interspecifically aggressive (Sedláček et al. 2004, Sedláček et al. 2006) but they also differed in their nestling diets.

The aim of the present study was to find out whether diet differences between the two species are a result of species-specific preferences or the diet composition of each species simply follows different food supply influenced by habitat composition of its territories and slightly different timing of breeding. We use the variance partitioning method based on multivariate Redundancy Analysis (RDA, Lepš & Šmilauer 2003) to test the influence of habitat, timing of breeding and the species of redstart on the composition of food brought to Redstart's and Black Redstart's nestlings. This method enables to ascribe the explained variance to particular explanatory variables (Lepš & Šmilauer 2003) and to separate their effects on the diet composition of coexisting bird species.

METHODS

Our study was carried out in the small town Březnice (3500 inhabitants) in Central Bohemia (Czech Republic, 13°56′E, 49°34′N). The study area (1.2 km^2) is a heterogeneous mosaic of diverse urban habitats — industrial sites, several types of built-up areas, sport fields, gardens, wooded streets etc. The study area includes three small and two larger parks (covering 0.4 km^2 in total), dominated by deciduous trees.

The diet of nestlings was studied using the neck-collar method (Rosenberg & Cooper 1990). Neck ligatures were applied once in each nest for a period of one and half hour. If there were not enough prey items collected from one sampling (minimum 30 prey items), second sample was taken one or two days later (5 cases in Redstart, 4 cases in Black Redstart) and both the samples were pooled for the analysis. Nestling diets were collected during the first breeding attempt in the season in 1999 and 2000. Samples from different breeding pairs were taken within the two following years (all adults were colour-ringed during the first year). The age of nestlings was similar in all the nests during sampling (8–11 days).

The prey items were identified down to the family level, and then grouped into 10 categories based on the taxonomy and life forms for further analyses (Isopoda, Araneida, Coleoptera adults/larvae, Hymenoptera adults/larvae, Lepidoptera adults/larvae, Diptera adults). Taxa comprising less than 5% of the diet were summarised under the category "Others".

We used the minimum convex polygon method (Ford & Myers 1981) to map the territories based on singing locations of males and foraging locations of males and females. We mapped the proportion of buildings, bare ground, sparse herb layer, short and dense herb layer, tall and dense herb layer, shrubs, tree cover (tree canopy projection on the ground), and water in each territory.

Differences in the diet composition of individual broods of the two redstart species (samples) were assessed using the Redundancy Analysis method (RDA, Lepš & Šmilauer 2003) in the program CANOCO 4.5. Biplots were visualised in CANODRAW 4.0 (ter Braak & Šmilauer 2002). RDA is a multivariate constrained ordination method originally designed for relating community species composition to underlying explanatory variables and provides a distribution-free Monte Carlo test of significance (Lepš & Šmilauer 2003).

In our analyses, community species composition is replaced by the diet composition of individual broods of the two redstart species. We tested the influence of the two species of redstart (each coded as 1 and 0), 8 habitat variables (proportion of habitats in each territory) and date of hatching (ranked as the order of the hatching date in the season, from 1 to 48, and called timing of breeding in further analyses) on the diet composition of individual broods. The proportional data were arcsin-transformed.

RDA was followed by variance partitioning (Lepš & Šmilauer 2003), a procedure enabling to ascribe the explained variance to particular explanatory variables. In this procedure, the influence of particular groups of variables (called covariables) is eliminated before the influence of the variables of interest (called explanatory variables) is tested. The use of partial analyses (i. e. analyses with covariables) enabled the separation of the effects of various explanatory variables on diet composition. This approach is similar to using covariates in ANCOVA. The significance of individual explanatory variables was tested separately and using the forward selection procedure (Lepš & Šmilauer 2003). The significance was evaluated by the Monte Carlo permutation test (499 permutations, see Lepš & Šmilauer 2003 for the details of permutation testing techniques).

RESULTS

We obtained 684 prey items from 10 Redstart nests (68.4 ± 32.4 prey items per nest) and 293 items from 8 Black Redstart nests (36.6 ± 7.3 prey items per nest). The average body length of prey (9.8 mm ± 4.7 in Restart, 10.2 mm ± 4.8 in Black Redstart) did not differ significantly between the two species (Student's t-test, $n_1 = 10$, $n_2 = 8$, $t = 0.35$, $p = 0.73$).

The overall food composition of the Redstart and Black Redstart is summarized in Fig. 1 (detailed data are also available on a request). Caterpillars (23.2%), Araneida (18.1%), Hymenoptera larvae (11.6%) and Isopods (10.9%) were the dominant prey of Black Redstart. On the other hand, adults of Coleoptera (18.1%), Hymenoptera (15.5%), Diptera (9.1%) and Lepidoptera (7.2%) dominated in Redstart diet.

The RDA ordination (Fig. 2) shows the differences in diet composition at the individual nests of the two restart species and correlation of explanatory variables with particular diet components. The first canonical axis clearly separates both redstart species (even if the species of redstart as a binary variable was left out). Some habitat characteristics of territories strongly correlate with the first axis as well. Buildings and bare ground on the right and trees and sparse herblayer on the left reflect the main differences in habitat composition of the two redstart species in the study area. Finally, the timing of breeding shows correlation with the redstart species. This reflects earlier breeding of the Black Redstart; nestlings hatched in average 19.0 days earlier than those of the Redstart in the study area.

The second RDA axis reflects mainly the differences in diet composition on individual nests of the Redstart. Adult Coleoptera and Diptera prevail in the nests with positive values on the second axis, the larger proportion of shrubs and water is correlated with presence of beetles and flies in Redstart diet. The nests situated amongst

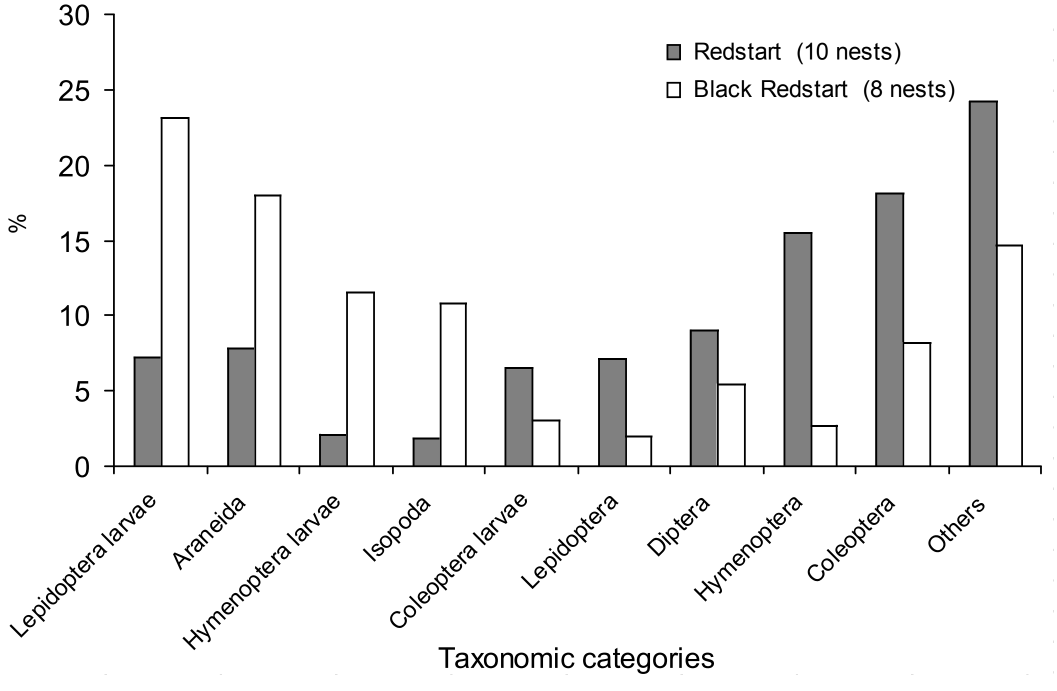

Fig. 1. The overall frequency distribution of taxonomic groups of prey brought to Redstart and Black Redstart nestlings.

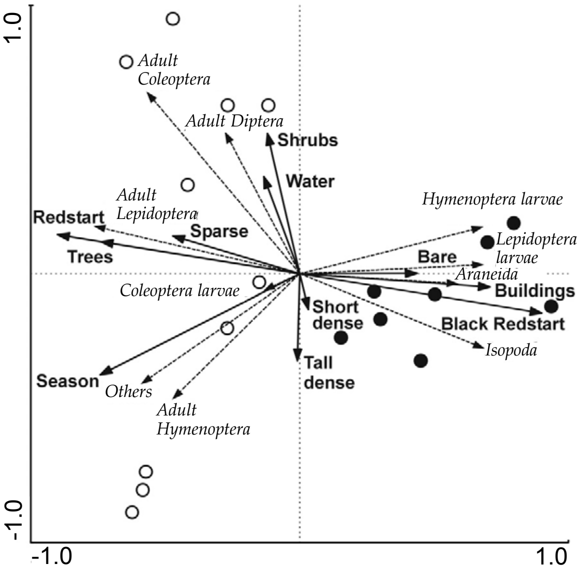

Fig. 2. Ordination diagram of RDA, with diet composition of Black Redstart and Redstart explained by habitat characteristics, timing of breeding and the species of redstart. Proportional data were arcsin transformed. Total variance accounted for all canonical axes is 70.6%. ● — Black Redstart broods, ○ — Redstart broods.

negative values of the axis contained larger proportion of adult Hymenoptera and rare prey (Others). There is only a weak correlation of these prey categories with the proportion of tall dense vegetation.

Separate testing of individual explanatory variables revealed the significant influence of the species of redstart, timing of breeding and proportion of buildings and trees in territories on the diet of the two redstart species (Table 1). Using the forward selection procedure, a minimum adequate model includes only one significant variable — the species of redstart (28.1% of explained variance, F = 6.25, p < 0.01). This is because the other variables, significant by independent testing, are correlated with the species of redstart. All explanatory variables explain 70.6% of the variance of diet composition.

Variance partitioning among particular explanatory variables is shown in Fig. 3. Almost a half of the explained variance (34%) results from habitat variables exclusively. The timing of breeding explains 8.9% of the variance and redstart species explains only 8.1%. The rest of explained variance (19.6%) cannot be separated and clearly attributed to individual explanatory variables.

The net influence of the species of redstart on diet composition after filtering out the effect of habitat and timing of breeding (used as covariables in the procedure) is shown in Fig. 4. The species of redstart correlates with the first axis. However, the influence of this variable on diet composition became nonsignificant (F = 1.93, p = 0.094) and the nests of the two species are mixed in the biplot. Most of the prey categories are more correlated with the second axis, which is not correlated with the species of redstart and represent the rest of variance.

DISCUSSION

An analysis of prey brought to nestlings by Black Redstarts and Redstarts in the area of sympatry revealed significant differences in the taxonomic composition of food, though there was no significant difference in sizes of prey items caught by the two redstart species. The most frequent prey of Black Redstart were the caterpillars,

Table 1. The influence of habitat characteristics, timing of breeding and species of redstart on the diet composition of Black Redstart and Redstart nestlings. Summary of multivariate analysis, the significance values obtained from the Monte Carlo permutation test with 499 random permutations.

Explanatory variable	Explained variance (%)	F	p-value
Species of redstart	28.1	6.253	0.002
Timing of breeding	21.7	4.440	0.002
Trees	19.6	3.897	0.004
Buildings	17.4	3.359	0.012
Bare ground	10.1	1.788	0.094
Sparse herb-layer	9.8	1.747	0.112
Shrubs	6.4	1.087	0.364
Water	4.4	0.729	0.614
Tall dense herb-layer	3.6	0.598	0.742
Short dense herb-layer	0.9	0.151	0.998

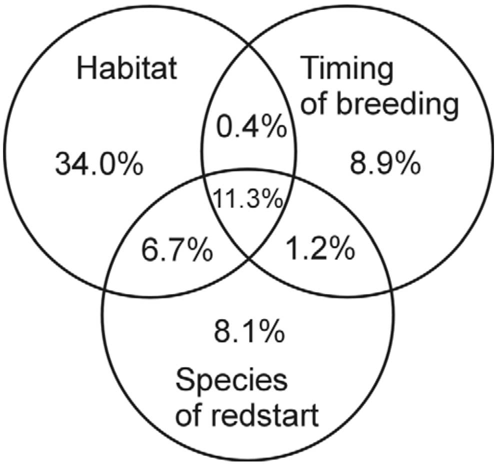

Fig. 3. Variance of Redstart and Black Redstart nestling diet explained by particular explanatory variables. RDA variance partitioning procedure. Total variance accounted for all canonical axes is 70.6%.

Araneida, Hymenoptera larvae and isopods. On the other hand, the Coleoptera, Hymenoptera, Diptera and Lepidoptera adults and Coleoptera larvae dominated in Redstart's diet. This result imply that the two redstart species segregate their diet niches in the area of sympatry. However, at the same time the two species used territories of different habitat composition in the study area. Black Redstarts occupied territories with larger proportion of buildings and sparse vegetation, whereas Redstarts preferred those covered by trees (Sedláček et al. 2004). Moreover, Redstart bred 19 days later in average than Black Redstart. We suggest that these environmental correlates could strongly affect the diet composition and therefore complicate a simple conclusion about the diet segregation between the two species in the area of their coexistence.

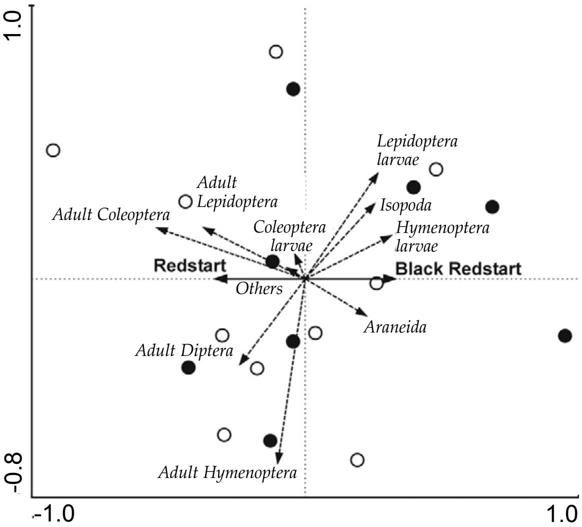

Fig. 4. Species differences of the diet composition of Redstart and Black Redstart nestlings after filtering out of the effects of habitat and timing of breeding (covariables in the analysis). RDA ordination results, proportional data were arcsin transformed. ● — Black Redstart broods, ○ — Redstart broods.

Therefore, we asked in further analyses, whether the observed interspecific differences in diet composition are caused by species-specific preferences of particular food types or are influenced mainly by differences in prey availability. Because we were unable to determine the food supply in particular territories directly, we used environmental correlates, which might affect it. The multivariate analysis followed by the variance partitioning procedure revealed that the most of the variance of food composition could be attributed to the habitat variables (34%) and the timing of breeding (8.9%). For example, adult Coleoptera and Diptera appeared frequently in the diet of those Redstart pairs with territories placed near water and containing larger proportion of shrubs (Fig. 2). The diet of the Redstart comprise more invertebrates, which become abundant later in the season, i. e. grasshoppers or adults of insects (e. g. winged ants, butterflies or Neuroptera and other minor groups of prey).

The filtering out the effects of habitat and timing of breeding indicated that the interspecific differences in diet composition are influenced only marginally by the species-specific diet preferences (8.1% of the explained variance). This analysis suggests that Redstarts and Black Redstarts are opportunistic insectivores feeding on the most frequent prey actually available within their territories.

If this is true, we predict that the two species vary in their foraging preferences depending on local conditions and food supply. We compared the food of Black Redstart and Redstart at all localities, where the diet composition was studied using the neck collar method (Fig. 5). The diet of the Redstart has been studied generally in several types of woods (Pfeifer & Keil 1958, Bösenberg 1960, Mansfeld 1961, Pruska 1980, Dornbusch 1971, Emmrich 1975), whereas most of studies on nestling diet of the Black Redstart have been carried out in towns (Mackrodt 1973, Mey 1974, Nicolai 1992, Krištín & Exnerová 1994), and mountain areas (Munteanu 1969).

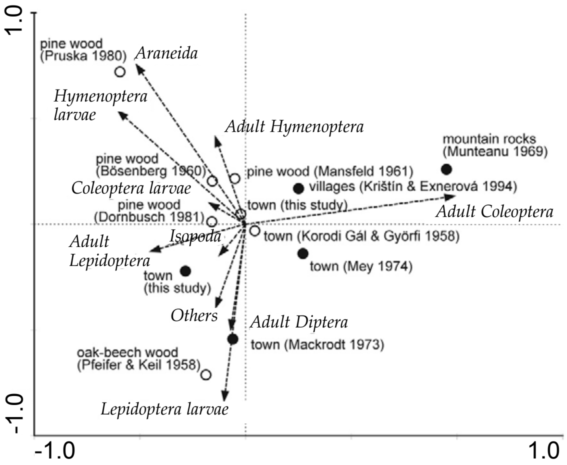

Fig. 5. Comparison of diet composition of Black Redstart and Redstart nestlings (neck collar method) in various habitats. PCA ordination results, variance accounted for the two axes is 66.4%. ● — Black Redstart broods, ○ — Redstart broods.

A comparison of diet from a variety of habitats and localities did not confirm species-specific preferences suggested in our study area. The diet is mainly influenced by environmental differences among studied localities, probably mainly by a degree of tree coverage. Specialisation to one or two types of prey is more characteristic of birds inhabiting natural habitats (woods as well as mountain rocks), whereas the food composition is more complex in urban settlements. On the other hand, there is no general tendency of the Black Redstart to catch arachnids, isopodes and Lepidoptera and Hymenoptera larvae more frequently than the Redstart does (see Figs 2 and 5 for comparison). This result confirms the conclusion made up on the basis of variance partitioning method. Therefore, we suggest that in the case of redstarts, the diet niche is apparently not enough sharply delimited to avoid competition for food. Although the two species occupy different habitats in the urban environment, we suggest that similar diet requirements could result in aggressive interactions in areas, where the two species come to close contact (Sedláček et al. 2004, Sedláček et al. 2006).

Food is the most important resource for which the birds compete. One possibility how to reduce interspecific competition is diet segregation in the areas of local sympatry (Martin 1987, Wiens 1989). This mechanism is well known in seed-eating birds and raptors (e.g. Schoener 1965, Grant 1986, Burton & Olsen 1997, Garcia & Arroyo 2005). However, there are only few cases of diet segregation in congeneric insectivorous birds (Cardenas et al. 1984, Cooper et al. 1990, Bureš 1994, 1995, Rolando & Laiolo 1997, Dyrcz & Flinks 2003). The results of our study showed that the diet segregation based only on comparison of diet composition could be deceptive. The diet differences between sympatric congeners could not be related only to differences in foraging preferences but mainly to their habitat use. We consider the variance partitioning method to be a powerful tool, which enables assessment of the sources of variance in diet, particularly in heterogeneous environments, where the pronounced variability in the food supply could be expected.

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STRESZCZENIE

[Skład pokarmu sympatrycznie występujących kopciuszka i pleszki w okresie lęgowym — preferencje gatunkowe czy odpowiedź na warunki środowiska?]

Zróżnicowanie zasobów pokarmowych jest jednym z ważniejszych sposobów na podział zasobów u ptaków. Jednakże wiele aspektów badań terenowych nad konkurencją o pokarm pomiędzy sympatrycznie występującymi gatunkami napotyka problemy metodyczne. Ptaki reagują na czasową i przestrzenną zmienność w dostępności zdobyczy, a dostępność pokarmu, która może być trudna do oszacowania silnie wpływa na skład pokarmu u ptaków.

W badaniach opisywano czy różnice w diecie piskląt stwierdzane pomiędzy sympatrycznie występującymi parami kopciuszka i pleszki są spowodowane przez preferencje gatunkowe czy też przez różną zasobność ich terytoriów.

Skład pokarmu badany był w mozaice środowisk miejskich, metodą obrączek okołogardłowych. Badaniami objęto 10 gniazd pleszki i 8 kopciuszka.

Wielkość zdobyczy nie różniła się istotnie między gatunkami, jednakże oba gatunki przynosiły bezkręgowce należące do innych grup systematycznych (Fig. 1). Gąsienice, pajęczaki, larwy błonkówek i równonogi dominowały w pokarmie kopciuszków, zaś chrząszcze, błonkówki, muchówki i motyle dominowały w pokarmie pleszek. Zastosowano podział wariancji w oparciu o metodę wielowymiarowej analizy redundancji w celu testowania wpływu habitatu, terminu przystępowania do lęgu i badanego gatunku na skład pokarmu piskląt (Fig. 2–4, Tab. 1). Oba gatunki wykorzystywały terytoria różniące się składem mikrośrodowisk. Kopciuszek zajmował terytoria z większym udziałem budynków i rzadkiej roślinności, podczas gdy pleszka preferowała środowiska zadrzewione. Stwierdzono także, że pleszki przystępowały do lęgów średnio 19 dni później niż kopciuszki.

Większość zmienności w pokarmie piskląt obu gatunków (70.6% wyjaśnianej zmienności dla obu osi korelacji kanonicznych), może być przypisywana zmienności środowiskowej (34%), oraz terminom lęgów (8.9%), podczas gdy tylko 8.1% zależało od gatunku (Fig. 4). W pracy porównano także istniejące dane dotyczące pokarmu piskląt kopciuszka i pleszki, zebrane w różnych środowiskach (Fig. 5).

Wyniki pracy sugerują, że skład pokarmu obu gatunków jest w większości zależny od chwilowej dostępności pokarmu, oraz w konsekwencji, że konkurencja międzygatunkowa jest unikania przede wszystkim przez utrzymywanie rozdzielnych terytoriów, niż wynika z rozdziału nisz pokarmowych.

Używana metoda podział wariancji wydaje się być odpowiednio czuła do wykorzystywania do analiz wpływu różnych zmiennych na skład pokarmu ptaków.