Ornis Fennica 80:71–78. 2003

Animals of different phenotype differentially utilise dietary niche — the case of the Great Grey Shrike *Lanius excubitor*

Martin Hromada, Lechosław Kuczyński*, Anton Krištín &
Piotr Tryjanowski

Hromada, M., Department of Zoology, University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic; and Department of Natural History, Šarišské Múzeum, Radničné nám. 13, SK-085 01 Bardejov, Slovakia
*Kuczyński, L., Department of Animal Morphology, Institute of Environmental Biology, Adam Mickiewicz University, 28 Czerwca 198, PL-61-485 Poznań, Poland. (*Corresponding author's e-mail: lechu@amu.edu.pl)*
Krištín, A., Institute of Forest Ecology, Slovak Academy of Sciences, Štúrova 2, SK-96 001 Zvolen, Slovakia
Tryjanowski, P., Department of Avian Biology & Ecology, Institute of Environmental Biology, Adam Mickiewicz University, Fredry 10, PL-61 701 Poznań, Poland

Received 3 February 2003, accepted 28 March 2003

We tested the morphological trait utility in Great Grey Shrike *Lanius excubitor*. The food composition was used as an indicator of phenotype performance advantage in utilising of particular dietary niche. Mounts and accompanying data (measurements and stomach contents) from the Slovak extensive collection, involving adult birds obtained from April to October, were selected for analysis (n = 48). Ordination methods (redundancy analysis) and Generalized Linear Model regression show that the composition of the bird's food was non-random in respect to body characteristics. Tarsus and wing lengths were the most important morphometric predictors and explained 12.7% of overall variance in food data. Smaller birds foraged mainly on Carabidae. Individuals with longer wings and tails more frequently preyed on flying and plant-dwelling insects. We conclude that phenotypic characteristics of an animal at least partially determine its diet.

1. Introduction

Variations in character form and function have been a subject of biology from its early beginnings. Darwin (1859) himself remarked that slight differences in the structure or habits of an organism can give it an advantage, and he argued that these differences, sometimes very subtle, provide the basis for natural selection. Alternative body forms are thought to affect the ability to exploit resources. Van Valen (1965) suggested that there is no single optimum phenotype in natural populations. Accordingly, variants in the population should differentially utilize parts of the foraging niche.

One of the crucial indicators of individual performance is foraging efficiency. Unsurprisingly, the majority of ecomorphological studies, both inter- and intraspecific, have focused on the correlation between morphology and diet. Intraspecific levels are best for analysing the mechanisms that link morphology and ecology (James 1982). However, there are methodological problems in the analysis of very small differences in structure, which may reflect individual and/or phenotype-specific differences in performance.

Intraspecific variation in foraging behaviour has previously been evaluated in several different contexts. Such variation has been attributed to (1) past experience of the forager, (2) temporal differences, (3) age- and sex-related differences, and, finally, (4) morphological differences (for overview see Price 1987). The majority of these studies were carried out on several populations of one species (e.g. Wiens & Rotenbery 1980, Schluter & Grant 1984), but see also Boag and Grant (1984) for a correlation between food size and morphology in the Darwin finch *Geospiza fortis*.

We chose a species with a complex foraging behaviour, the Great Grey Shrike *Lanius excubitor*, for testing the relationship between morphology and foraging. Shrikes orient most of their hunting forays towards the ground; less frequently they hunt flying or vegetation-dwelling prey. Moreover, shrikes are versatile predators with a wide food niche, able to feed on a wide range of prey species and to specialise or generalise depending on local conditions (Cade 1995). We tested the hypothesis that individual Great Grey Shrikes with different phenotypes catch prey with different ecological characteristics, such as size, place of occurrence or mobility.

2. Methods

2.1. Data collection

Dataset analysed is based on an extensive collection of the Great Grey Shrike mounts (skins) from the Šarišské Museum Bardejov (SMB), Slovakia (Hromada *et al.* 2003). Birds were collected in the region of NE Slovakia (49°3–27′N 20°30–34′E), all localities were in similar habitats with alike prey assemblage (Hromada & Krištín 1996, Hromada *et al.* 2003), therefore habitat and food offer dependent biases we assume not to be important in analyse. Individuals included in the analysis were collected in the period 1958–1964. Although stomach contents were available from specimens throughout the year (total 133 stomachs), only material obtained from April to October was analysed in order to avoid seasonal biases. During this period, all food classes are present in food, including flying, ground- and vegetation-dwelling invertebrates. In winter all birds feed predominantly on small mammals (for diet composition and dynamics see Hromada & Krištín 1996). Only adult birds were included in the analysis (n = 48, 25 males, 15 females and 8 unsexed), because the ability of young birds to catch different prey types can be affected by experience.

Variables in the statistical analysis were selected for their presumed correlation with the ability of the bird to hunt effectively. The principal function of (1) wings and (2) tail is to generate lift (Balmford *et al.* 1993). Thus, changes in their size and/or shape should affect the capability of the animal to fly and manoeuvre (e.g. Leisler 1980, James 1982, Nystrom 1991, Fitzpatrick 1999). Intraspecific importance of (3) bill size and shape has been shown, for example, in Darwin finches, to be as important as body size (Boag & Grant 1981, 1984, Price 1987). We also used (4) body mass and (5) tarsus length, which are assumed to be overall body-size indicators (Brown 1996). Shrikes do not use the tarsus during hunting and only occasionally in prey handling (Cade 1995, our unpublished data).

Patterns in food composition correlates can be a side-effect of allometric relationships among body traits (James 1982). Therefore, we explored correlations between bird measurements. The important feature of our dataset is that all birds were measured by the same method and person (Tibor Weisz, 1928–1983), who was not aware of a future use of the data. The collection of the birds was not selective in any sense. All measurements were taken on freshly obtained birds. Lengths of both wings, body, tail and bill were measured in the same way to that of Svensson (1992). Tarsus was taken as the distance between sole side of opened foot, abutted on calliper at right angle and measured to the proximal point of tarsometatarsus. Feather measurements (body, wing, tail) were taken with an accuracy of 0.5 mm, bone measurements (bill, tarsus) to 0.05 mm. Specimens were weighed to within 0.5 g.

Stomachs were collected during dissections that were performed shortly after collection of the bird and stored in 75% ethylalcohol. Because the Great Grey Shrike diet consists of several tens of prey species, we pooled the prey items into taxonomic/ecological groups. Only prey types taxonomically related and with similar ecological characteristics were pooled (Table 1). This approach not only makes statistical analysis more reliable but, we assume, it also better reflects foraging strategy of an individual animal. Stomach contents, which we used, in contrast to pellets and observations, are appropriate for such kind of analyses from statistical point of view, because the samples are totally independent.

2.2. Data analysis

To examine our data we used multivariate ordination statistics, which allow the relationship between several explanatory variables and multiple explained variables to be tested en bloc. An advantage of this approach is that it also permits the exploration of inter-correlations between particular variables in a complex data matrix which could be otherwise unrevealed.

Constrained ordination methods were applied (Ter Braak & Prentice 1988) to investigate intraspecific differences in foraging methods among individuals of Great Grey Shrike. These modern multivariate methods, currently widely used mainly in community ecology and botany, are only occasionally used in zoological studies despite their great explanatory potential, as well as possibility to test hypotheses. We used CANOCO 4.02 software to perform the analyses (Ter Braak & Šmilauer 1998).

Fisher Linear Discriminant Function (FLDF) was used for testing the influence of sex and season on food composition.

First, linearity of the response of explained variables (food composition) to explanatory variables (measurements of an animal) was tested. The length of the longest gradient in Detrended Canonical Correspondence Analysis (DCCA) was 2.121; therefore we decided to use a linear method, the Redundancy Analysis (RDA) (Lepš & Šmilauer 1999). The ordination diagrams display scores of response (prey types) and quantitative explanatory variable (morphometric characteristics of the bird), both represented as arrows.

Significance of the multivariate model for all canonical axes was tested using Monte Carlo Permutation Test (MCPT) under the full model; 5000 repetitions were performed, as recommended by Manly (1991).

We explored the significance of the correlation between particular bird measurements and food composition initially by means of forward selection. Only measurements with $P \leq 0.1$ were used in the overall model, as commonly practised in ordination statistics. This technique enables one to choose the variables which explain the highest amount in food data (Lepš & Šmilauer 1999).

Table 1. Food composition of *Lanius excubitor*, based on analysis of stomach contents (n = 48).

	n	n %	F	F %
Porcelio sp.	3	1.52	1	2.08
Araneida	2	1.02	2	4.17
Xysticus sp.	1	0.51	1	2.08
Gryllotalpa gryllotalpa	15	7.61	11	22.92
Gryllus campestris	1	0.51	1	2.08
Tettigoniidae	7	3.55	5	10.42
Chorthippus sp.	7	3.55	4	8.33
Heteroptera	7	3.55	7	14.58
Coleoptera larvae	2	1.02	2	4.17
Carabidae >20 mm	5	2.54	4	8.33
Carabidae 10-20 mm	50	25.38	17	35.42
Carabidae <10 mm	5	2.54	4	8.33
Byrrhus sp.	1	0.51	1	2.08
Silphidae	15	7.61	6	12.50
Meloe sp.	1	0.51	1	2.08
Scarabeidae >10 mm	1	0.51	1	2.08
Melolontha melolontha	2	1.02	2	4.17
Aphodius sp.	3	1.52	3	6.25
Onthophagus sp.	2	1.02	2	4.17
Geotrupes sp.	3	1.52	3	6.25
Lepidoptera larvae	4	2.03	3	6.25
Lepidopera imagoes	2	1.02	1	2.08
Bees & wasps	15	7.61	8	16.67
Bombus sp.	3	1.52	2	4.17
Formicidae	1	0.51	1	2.08
Tipula sp.	5	2.54	1	2.08
Aves	1	0.51	1	2.08
Lacerta sp.	1	0.51	1	2.08
Microtus arvalis	32	16.24	31	64.58
Total	197	100.00	48	100.00

Measurements which did not fulfil criteria of forward selection were included in the model as supplementary variables in the detection of correlations of phenotypic traits and food composition.

The method of variance partitioning was used to separate effects of individual morphometric traits on food data (Borcard *et al.* 1992).

CANOCO's Generalized Linear Model (GLM) module was employed for testing the relationship of particular food types to individual morphometric characteristics (Ter Braak & Šmilauer 1998). GLM regressions with Poisson distribution family and Log link function were used. We computed a variance explained by the model as the difference between the null model and a fitted model deviance (McCullagh & Nelder 1989).

We used Bonferroni correction for adjusment of experimentwise α level (Chandler 1995) for multiple analyses of correlations between particular measurements of the birds, as well as relationships between particular bird phenotype and numbers of prey consumed.

3. Results

3.1. Preliminary analyses

Sexes did not differ in respect to the food composition (FLDF, F = 0.99, P = 0.520). Therefore, data from all birds were pooled together for further analyses. Similarly, there was no significant differences between food composition with respect to season (FLDF, P > 0.05 in all cases).

Body mass was not correlated with any measurement. Other measurements were significantly correlated, the strongest being between tail and wing length (Tables 2 and 3).

Table 2. Means, standard deviations and 95% confidence limits (LCI-lower, UCI-upper) of Great Grey Shrike measurements (n = 149).

Trait	Mean	SD	LCI	UCI
Mass (g)	67.83	4.75	67.04	68.62
Tarsus length (mm)	26.37	0.73	26.25	26.50
Wing length (mm)	113.17	2.33	112.77	113.56
Tail length (mm)	115.65	3.75	115.03	116.28
Bill length (mm)	17.96	0.89	17.80	18.11

In total 197 prey items were identified in the stomachs of examined birds. The number of preys per stomach was in the range 1–14 (Mean = 4.10, Median = 3.00, SD = 2.93) (Table 1).

3.2. Phenotype *vs.* food composition — RDA ordination

RDA revealed a significant relationship between food composition and phenotypic characteristics in the studied species (F = 2.78, significance of all canonical axes P = 0.009) (Fig. 1). Tarsus and wing lengths were included in the model after forward selection (P = 0.016 and P = 0.056, respectively). Body mass, tail and bill lengths did not fulfil criteria of forward selection.

There are strong correlations of bird body characteristics and food composition. The measurements divided naturally into two highly negatively correlated groups in RDA (Fig. 1a, b). In the first group wing length is strongly positively correlated with tail length and bill length. In second group tarsus length is correlated with body mass. Composition of the food is non-random in respect to body characteristics. Long-winged individuals tended to catch more bees and wasps, Heteropera and mole cricket *Gryllotalpa gryllotalpa*, and fewer Field Voles *Microtus arvalis*. Large birds with long tarsi caught more crickets Tettigoniidae and carrion beetles Silphidae and fewer bees and bugs Heteroptera (Fig. 1 a, b). Birds with smaller measurements all-round caught more middle-sized ground beetles Carabidae.

All bird measurements in model would explain 16.8% of overall variance in food composition

Table 3. Correlation matrix of the Great Grey Shrike measurements (n = 149). Significance level adjusted after Bonferroni correction at α = 0.005. Coefficients significant at the level P ≤ 0.05 are indicated with asterisks.

Trait	Wing length	Tail length	Bill length	Tarsus length
Body mass	0.17	–0.10	–0.02	0.16
Wing length	–	0.60*	0.32*	0.31*
Tail length		–	0.37*	0.32*
Bill length			–	0.27*

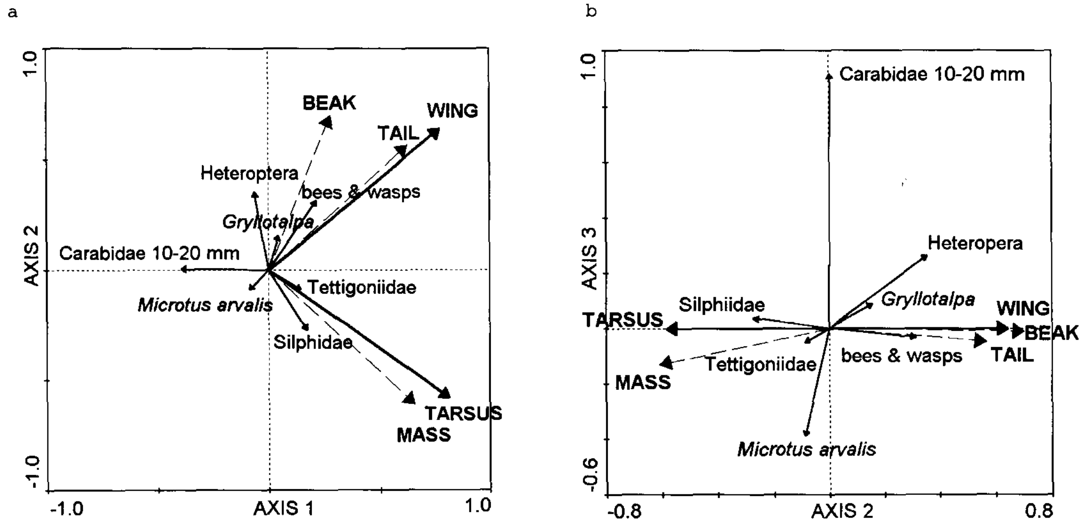

Fig. 1. Ordination diagram (RDA) of the Great Grey Shrike food spectrum, based on analysis of stomach contents (n = 48). The morphometric characteristics of birds are used as predictors of presence of prey type in animal of particular phenotype. MCPT with 5000 repetitions. Tarsus and wing lengths were included into the model after forward selection (P = 0.016 and P = 0.056, respectively, solid arrows). Supplementary variables (dashed arrows) visualise correlations among phenotypic traits in dependency on the food composition. Overall model F = 2.78, significance of all canonical axes P = 0.009. Only prey items present in at least 10% of stomachs are visualized. The angles among the species arrows approximate the linear correlation coeficients between the species. The correlation between two species is equal to the cosine of the angle between two species arrows. A projection point near the zero point corresponds to an average value of variable (Lepš & Šmilauer 1999).

data. However, the model with only traits identified in forward selection explained 12.7% of overall variance, with residual variability of 87.3%. The variability explained by this model was analysed by variance partitioning. Particular variables then represent portions of variability as follows: tarsus length 38.3% and wing length 35.4%, which together match 9.4% of overall variability. The residual of 26.3% from variance explained attributes mutual affect of both explanatory variables included in the model.

3.3. Phenotype *vs.* foraging — GLM regression

Correlations between body measurements and food composition in GLM model showed a similar pattern to those in RDA (Table 4, Fig. 2). Mass

Table 4. Relationship of specific prey and bird phenotype (GLM). Only prey types present in more than 10% of animals were tested. EV = explained variance. Experimentwise significance level adjusted after Bonferroni correction at $\alpha = 0.007$. Significant regressions indicated with asterisks.

	Mass		Tarsus		Wing		Tail		Bill	
	EV %	p	EV %	p	EV %	p	EV %	P	EV %	p
Carabidae 10–20 mm	10.29	<0.001*	14.83	<0.001*	14.65	0.001*	7.93	0.002*	2.12	0.100
Gryllotalpa	3.04	0.211	0.38	0.330	2.40	0.293	5.71	0.107	3.76	0.190
Heteroptera	1.70	0.499	10.2	0.103	4.34	0.283	2.22	0.442	8.34	0.140
Microtus arvalis	1.67	0.489	0.00	0.062	1.00	0.411	0.55	0.311	3.23	0.339
Silphidae	18.25	0.001*	16.97	0.001*	0.36	0.373	1.55	0.316	24.09	<0.001*
Tettigonia	6.92	0.158	5.21	0.219	0.57	0.311	0.168	0.177	7.56	0.140
Bees & wasps	4.90	0.115	0.00	0.050	18.18	0.003*	15.47	0.005*	0.67	0.448

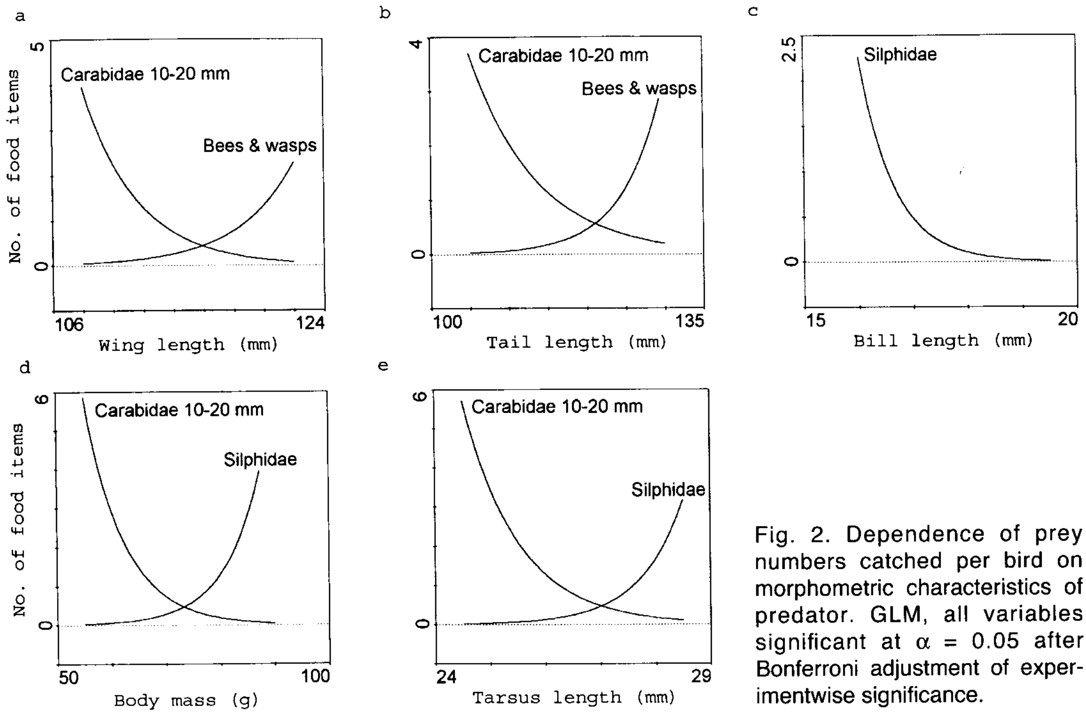

Fig. 2. Dependence of prey numbers catched per bird on morphometric characteristics of predator. GLM, all variables significant at α = 0.05 after Bonferroni adjustment of experimentwise significance.

and tarsus length were negatively correlated with number of middle-sized Carabidae. Both traits are positively correlated with the number of Silphidae. Tail and wing lengths showed a positive correlation with bee and wasp numbers. By contrast, birds with short wings and tails caught more Carabidae. The only food type correlated with bill length were Silphidae; the relationship between both variables was negative.

4. Discussion

4.1. Morphology affects ecology

We assumed in this study that number of prey items of particular type in stomach content can be an indicator of foraging efficiency. The effect of morphological data on food composition shows a distinct pattern. Morphological data, if used as a predictor of individual bird diet, create two well-defined groups. These groups of traits are not correlated in the same way, as raw morphometric data. This indicates the existence of an effect of individual morphology on performance, and, by contrast, eliminates the possibility of an effect of allometry (James 1982).

4.2. Effect of a phenotype

Smaller birds (in all measurements) caught Carabidae beetles with higher efficiency. Carabidae create an ordination diagram group segregated from all others. Smaller birds could be less capable aerial foragers and foragers on large, more mobile prey. Thus they select distinct and slow ground beetles, which, although not providing a high energetic profit, are the easiest available prey.

The relationship of wing and tail to flight performance and manoeuvrability is well known (Leisler 1980, Fitzpatrick 1999). Intraspecific studies revealed that birds with longer wings more frequently performed fly-catching behaviour, and birds with less pointed wings are better adapted for hovering (Nystrom 1991). We suggest a similar relationship: birds with longer wings seem to be better in aerial foraging. However, the similar pattern in wing and tail measurements in GLM as well as RDA can be caused by a narrow allometric relationship between them, considering the high correlation between both traits.

Although a correlation of the wing and tail length with foraging efficiency on *Microtus arvalis* is not significant in regression, the position of this prey in ordination diagrams is interesting. The shorter wings are known to be more appropriate for hunting running prey in raptors (Tornberg *et al.* 1999). It seems that no other morphological trait, including overall size, affects a bird's ability to catch a vole.

Body mass and tarsus length are overall indicators of avian body size (Brown 1996). We did not find a clear correlation of prey size with Great Grey Shrike size, although in the ordination diagram of third against second ordination axis there are more large prey types distributed with larger birds than smaller. However, in GLM regressions only middle-sized Carabidae are significantly related to the bird's size, as already discussed, and silphid beetles. Reasons for the relationship between this prey type and morphology can only be speculated.

Bill length does not significantly influence the composition of food in gradient analysis, probably because the relationship of bill morphology and food characteristics are more complicated (Boag & Grant 1984, Brandl *et al.* 1994).

The overall variance in food composition data, explained by two morphometric traits included in the ordination model, is 12.7%. The residual variability in the food composition data, reaching 87.3%, would be caused by other factors influencing foraging efficiency. Inner factors, such as state of health and experience, along with external factors such as habitat, weather, daytime, prey susceptibility and others must have basic influence on foraging efficiency. Portions of the variance explained by particular traits are moderate, and account for 4.9% (tarsus) and 4.5% (wing) of the variability explained by the model. Nevertheless, we consider the fact that morphology explains almost 13% of dietary variance to be very interesting.

Our results suggest that particular phenotypes within one population could be separated by fitness valleys, more or less distinct. Phenotype dependent differences in the utilising of the ecological niche are extremely important for explaining a phenotypic divergence within population, and could help us to determine why such divergence proceeds in one direction and not another. Investigation of trait utility, the performance advantages of specific trait values, in particular niche portion, we suggest to be promising in the identifying and study of evolution on population and species level.

Acknowledgements: We are most grateful to N. Collar, T. Grim, M. Konvička, J. Lepš, P. Lundvall, P. Šmilauer and R. Tornberg for valuable comments and discussions. We thank all employees of Šarišské Museum Bardejov, Slovakia for their support of our work. MH was supported by A. Mickiewicz University Poznań grant in 1999 and 2001 and research fellowship in 2000, and SGA of University of South Bohemia České Budějovice, Czech Republic. LK and PT were partially supported by a grant from the Faculty of Biology Adam Mickiewicz University, GEF/SGP Poland and KBN grant (6 PO4F 04621). AK was partially supported by a grant from the Slovak Grant Agency No. 2/3006/23.

Selostus: **Ilmiasultaan erilaiset lapinharakkayksilöt käyttävät erilaista ravintoa**

Artikkelin kirjoittajat tutkivat lapinharakan fenotyypin, ilmiasun, vaikutusta lintujen ravinnon koostumukseen. Aineistona käytettiin slovakialaisen museon lapinharakkanäytteistä kerättyjä morfometrisiä tietoja sekä mahalaukkujen sisältöjä. Kaikki mittaukset teki sama henkilö "tuoreista" linnuista. Aineistoon kelpuutettiin mukaan vain huhti-lokakuussa kuolleet aikuiset yksilöt. Tutkimusaineisto koostui 48 yksilöstä, joista 25 oli koiraita, 15 naaraita ja 9 yksilön sukupuolta ei oltu määritetty. Linnuista oli mitattu siiven, pyrstön ja nilkan pituudet, nokan koko ja muoto sekä linnun paino. Lisäksi oli analysoitu vatsalaukun sisältö. Sukupuolella tai vuodenajalla ei havaittu olevan vaikutusta ravinnon koostumuksen, joten aineisto yhdistettiin jatkoanalyysejä varten. Lapinharakan mahalaukusta löytyi keskimäärin 4,1 saalisyksilöä. Tutkimuksessa havaittiin, että linnun fenotyyppi vaikutti yksilön käyttämän ravinnon koostumukseen. Nilkan ja siiven pituudet olivat tärkeimmät lapinharakan ravinnon koostumusta selittävät morfologiset tekijät. Pienikokoiset lapinharakkayksilöt olivat saalistaneet pääasiassa maakiitäjäisiä. Pitkäsiipiset ja -pyrstöiset yksilöt olivat puolestaan saalistaneet useammin lentäviä ja kasvillisuuden kätköissä piileskeleviä hyönteisiä. Kirjoittajat päättelevät, että yksilön ilmiasu ainakin osittain määrää yksilön käyttämän ravinnon koostumusta.

References

Balmford, A., Jones, I. L. & Thomas, A. D. L. 1993: On avian asymmetry: the evidence of natural selection for symmetrical tails and wings in birds. — Proc. R. Soc. Lond. B 25: 245–251.

Boag, P. T. & Grant, P. R. 1981: Intense natural selection on a population of Darwin's Finches (Geospizidae) in the Galapágos. — Science 214: 82–85.

Boag, P. T. & Grant, P. R. 1984: Darwin's finches (Geospiza) on Isla Daphne major, Galápagos; breeding and feeding ecology in a climatically variable environment. — Ecol. Monogr. 54: 463–489.

Borcard, D., Legendre, P. & Drapeau, P. 1992: Partialling out the spacial component of ecological variation. — Ecology 73: 1045–1055.

Brandl, R., Krištín, A. & Leisler, B. 1994: Dietary niche breadth in a local community of passerine birds: an analysis using phylogenetic contrasts. — Oecologia 98: 109–116.

Brown, M. E. 1996: Assessing body condition in birds. — Current Ornith. 13: 67–135.

Cade, T. J. 1995: Shrikes as predators. — Proc. West. Found. Vert. Zool. 6: 1–5.

Chandler, C. R. 1995: Practical considerations in the use of simultaneous inference for multiple tests. - Abim. Behav. 49: 524–527.

Darwin, C. 1859: The origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. — Murray, London. 703 pp.

Fitzpatrick, S. 1999: Tail length in birds in relation to tail shape, general flight ecology and sexual selection. — J. Evol. Biol. 12: 49–60.

Hromada, M. & Krištín, A. 1996: Changes in the food of the great grey shrike (Lanius excubitor) during the year. — Biologia 51: 227–233.

Hromada, M., Kuczyński, L., Skoracki, M., Antczak, M. & Tryjanowski, P. 2003: The value of the bird collections and associated data in regional museums: Lanius excubitor specimens in Sarisské Museum, Bardejov, Slovakia. — Bull. Brit. Orn. Cl., Supplement 123A: 226–233.

James, F. C. 1982: The ecological Morphology of birds: a review. — Ann. Zool. Fennici. 19: 265–275.

Leisler, B. 1980: Morphological aspects of ecological specialization in bird genera. — Ökol. Vögel 2: 199–220.

Lep , J. & Šmilauer, P. 1999: Multivariate Analysis of Ecological Data. — University of South Bohemia, České Budějovice, Czech Republic. 102 pp.

Manly, B. F. J. 1991: Randomization and Monte Carlo methods in biology. — Chapman & Hall. 296 pp.

McCullagh, P. & Nelder, J. A. 1989: Generalised Linear models. Second Edition. — Chapman and Hall, London. 511 pp.

Nystrom, K. G. K. 1991: On sex-specific foraging behavior in the willow warbler, Phylloscopus trochilus. — Can. J. Zool. 69: 462–470.

Price, T. 1987: Diet variation in a population of darwins finches. — Ecology 68: 1015–1028.

Price, T. D., Grant, P. R., Gibbs, H. L. & Boag, P. T. 1984: Recurrent patterns of natural-selection in a population of darwin finches. — Nature 309: 787–789.

Schluter, D. & Grant, P. R. 1984: Ecological correlates of morphological evolution in a Darwin's finch, Geospiza difficilis. — Evolution 38: 856–869.

Svensson, R. L. 1992: Identification guide to European passerines. — Zoolog. Museum, Stockholm. 368 pp.

Ter Braak, C. J. F. & Prentice, I. C. 1988: A theory of gradient analysis. — Advances in Ecological Research 18: 93–138.

Ter Braak C. J. F. & Šmilauer, P. 1998: CANOCO Reference Manual and User's Guide to CANOCO for Windows. — Microcomputer Power, Ithaca, USA. 353 pp.

Tornberg, R., Mönkkönen, M. & Pahkala, M. 1999: Changes in diet and morphology of Finnish goshawks from 1960s to 1990s. — Oecologia 121: 396–376.

Van Valen, L. 1965: Morphological variation and width of ecological niche. — Amer. Nat. 98: 377–390.

Wiens, J. A. & Rotenberry, J. T. 1980: Patterns of morphology and ecology in grassland and shrubsteppe bird populations. — Ecol. Monog. 50: 287–308.