

# Diet composition and prey choice by the red-backed shrike *Lanius collurio* in western Poland

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**ABSTRACT.** We investigated diet and prey choice in a population of red-backed shrike (*Lanius collurio*) living in an intensively used farmland (W Poland). Diet was estimated by three methods : collars in nestlings, and pellets and prey remains in larders. Insects, mainly Coleoptera, Hymenoptera and Orthoptera constituted 97.7% of the diet, with a total of 4392 prey items identified from all samples. However, during rainy and cold days vertebrates formed an important component (up to 26.5% by biomass) of the food of the red-backed shrike.

Food preference – expressed in relation to availability – was estimated for five arthropod taxa. Hymenoptera, Orthoptera and Coleoptera were more preferred prey. Heteroptera and “other invertebrates”, included mainly flies, dragonflies and spiders were less preferred.

For rational management of the red-backed shrike in farmland, we suggest that places with available prey (in appropriate densities), small vegetation patches and perches suited to low-expenditure hunting strategy, should be preserved, as well as established.

**KEY WORDS :** diet, food selection, insects, vertebrates, *Lanius collurio*.

## INTRODUCTION

The red-backed shrike *Lanius collurio* (Linnaeus, 1758) is the most numerous of the shrike species to breed in the Western Palaearctic. However, decline of the local populations over many areas within the geographical range of the species has been primarily attributed to a loss of suitable habitat. Changes in agricultural practices were thought to be partly responsible for a reduction of breeding and foraging habitats in farmland (LEFRANC, 1997; LEUGGER-EGGIMANN, 1997). Moreover, some authors showed by modelling that potential food sources have a critical role in changes in local population size of the red-backed shrikes (LEUGGER-EGGIMANN, 1997; SCHIFFERLI et al., 1999; KUPER et al., 2000) and consequently used this knowledge in conservation programs for this declining and endangered species.

The red-backed shrike is mainly an insectivorous bird; sometimes the diet is supplemented by vertebrates (LEFRANC & WORFOLK, 1997). However, data on prey preferences is still lacking, except from one study in Spain (HERNANDEZ et al., 1993). Moreover, data on the contribution of vertebrates to the diet of red-backed shrike are speculative, as studies focused on vertebrate use only, not within the context of the entire diet spectrum (KNYSH, 1982; HERNANDEZ, 1995).

Therefore, in this study we focused on (1) describing diet composition of the red-backed shrike in a farmland area, paying particular attention to the use of vertebrate prey and (2) prey selection.

## MATERIAL AND METHODS

### Study area and birds

The research was carried out during the period from July 1999 to August 2000 in the central Wielkopolska Province, western Poland, which is situated near town of Poznań. The region is dominated by agricultural lands, and habitats include cultivated fields (80%), small forests (15%), marshlands (3%) and inhabited areas. Most red-backed shrikes arrive in the Wielkopolska region in early May (TRYJANOWSKI & SPARKS, 2001), start breeding between mid May and mid June (KUŹNIAK, 1999; TRYJANOWSKI et al., 2000), and leave the study area in September or October. The study area was ca 60 km<sup>2</sup>, with a mean density of 1.1 – 1.4 breeding pairs/km<sup>2</sup>. For further details on the study area and the biology of the red-backed shrike see KUŹNIAK & TRYJANOWSKI (2000) and TRYJANOWSKI et al. (2000).

### Food analyses

Three methods were applied simultaneously to analyse diet composition and to predict prey choice (TRYJANOWSKI et al., 2003).

Food of nestlings was assessed by collar samples when the young were 5 to 10 days old. After every two to three feeding visits by the parents, the food was removed from the nestlings' throats with forceps. A total of 66 prey items were collected from 12 nests. Arthropods were preserved in ethanol (70%) and identified to the family level, using a reference collection obtained from the same study area (J. KARG, unpublished data).

Pellets were collected from 17 shrike territories. A total of 3832 prey items were identified (at least to family level) in 336 pellets. Pellets were analysed by a standard procedure (ROSENBERG & COOPER, 1990).

We also monitored larders and butchering points, where the shrikes prepare food for nestlings, as well as for themselves (LEFRANC & WORFOLK, 1997). We used data from 14 such points, with a total of 594 prey items removed from larders.

### Available food

Because the red-backed shrikes prey mainly on invertebrates (for details see Results), only data for invertebrate prey were collected. A modified quick-trap method was used (RYSZKOWSKI & KARG, 1977). Samples were taken by covering 0.25 m<sup>2</sup> of the ground with a cage without a bottom (so called biocenometer). In six territories of red-backed shrike with places of higher shrike foraging activity, samples (10 in each control) were taken five times over the period June – August. Insects and spiders were collected from under the net by a vacuum sampler.

Data are presented as means for the whole study area during the breeding period, and are expressed as the number of individuals and/or biomass per m<sup>2</sup>.

### Calculations and statistics

Dry mass of invertebrates (after RYSZKOWSKI & KARG, 1977) was used for this analysis.

Prey choice analyses were carried out using compositional analysis of the five numerically dominant taxa: beetles (Coleoptera), bees and wasps (Hymenoptera), orthopterans (Orthoptera), bugs (Heteroptera), and a category containing all the remaining taxa referred to as “others” (moths and butterflies Lepidoptera, flies Diptera, spiders Araneae and many others – for details see Results).

To assess shrike selection of particular groups (orders) of insects, Ivlev's selectivity index (*D*) was calculated, as modified by JACOBS (1974):  $D = (r-p)/(r+p-2rp)$ , where *r* denotes the fraction of a given group of insects in the total number of insects identified from pellets, and *p* – the fraction of a group of insects in the insect community. *D* varies from -1 (negative selection) to 0 (catching proportional to abundance), to 1 (positive selection).

The analysis of prey choice was done in six territories only, where data on the red-backed shrike diet were collected using all three methods and the information on density of prey was available.

Because data on vertebrates in the red-backed shrike diet were limited, we decided to enlarge the study plot to include habitats located around it. Success of vertebrate catching was investigated using  $\chi^2$  - test, with two daily groups: with and without rain. Daily precipitation data for the study period were obtained from the Turew local meteorological station, located in the centre of the study area.

Standard statistical methods were used according to ZAR (1999). All statistical tests were two-tailed.

## RESULTS

### Invertebrates

Invertebrates constituted 98.9% of all (*N* = 4392) prey items, but 73.5% of dry mass from 415 g biomass consumed (Table in appendix). In general, the two methods of assessment of food contents, by number of individual prey items and by biomass, were highly positively correlated ( $r_s = 0.752$ , *n* = 150 prey categories, *p* < 0.0001).

Over 51% of the prey items were beetles; dung (Scarabeidae) and ground (Carabidae) beetles accounted for almost a third of the prey. Hymenoptera, with ants (Formicidae), ichneumon flies (Ichneumonidae), bees (Apidae) and wasps (Vespidae), made up around 22% of the diet. A third and a fourth group were grasshoppers and crickets (Orthoptera: Tettigonidae and Acrididae) and bugs (Heteroptera), representing respectively 12.9 and 7.2% of the diet. The group labelled “others” invertebrates and vertebrates accounted together for only approximately 7%. Pattern of prey use by biomass is similar, although with more important roles for orthopterans and vertebrates (Fig. 1 A & B).

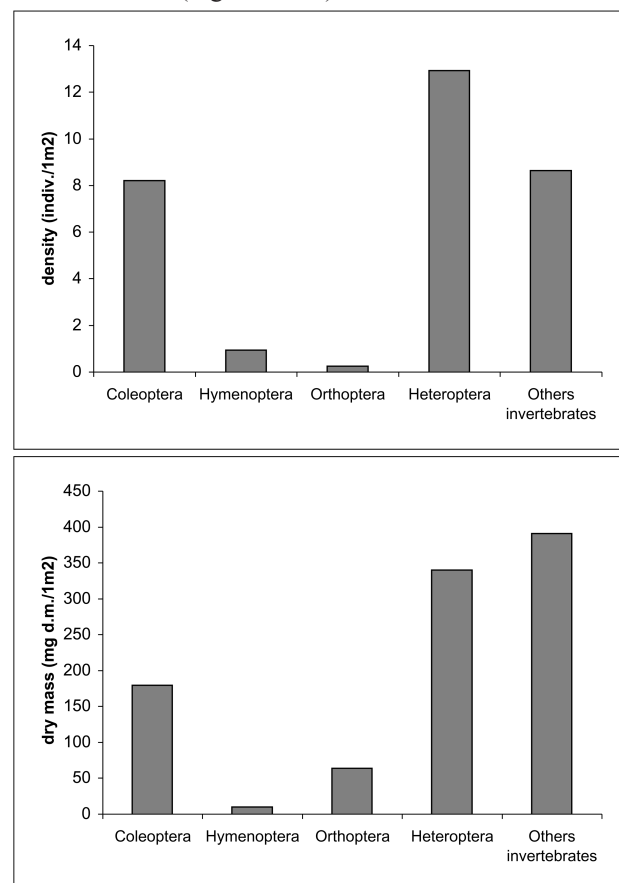


Fig. 1. – Percent composition of the red-backed shrike diet in terms of number of prey (A-top) and biomass (B-bottom).

### Vertebrates

A total of 64 vertebrate prey caught by the red-backed shrike were recorded (Table 1). Small mammals constituted the main prey item (over 80%). Vertebrates were more often predated on cold and rainy days, than on days without rain (*p* < 0.0001).

TABLE 1

Vertebrates in the diet of the red-backed shrike in Wielkopolska Province, Poland. All methods complied.

Prey item	N individuals	%
<i>Microtus</i> sp.	29	45.3
<i>Apodemus</i> sp.	11	17.2
<i>Mus musculus</i>	1	1.6
<i>Sorex</i> sp.	11	17.2
Micromammalia total	52	81.3
<i>Emberiza citrinella</i>	4	6.3
<i>Parus caeruleus</i>	1	1.6
Passeriformes indet.	1	1.6
Aves total	6	9.4
<i>Lacerta</i> sp.	3	4.7
<i>Rana</i> sp.	3	4.7
Vertebrates total	64	100

### Prey choice

The main potential food consisted of bugs (Heteroptera), by number of individuals, and other invertebrates (this category included mainly flies and dragonflies) by biomass (Fig. 2 A & B).

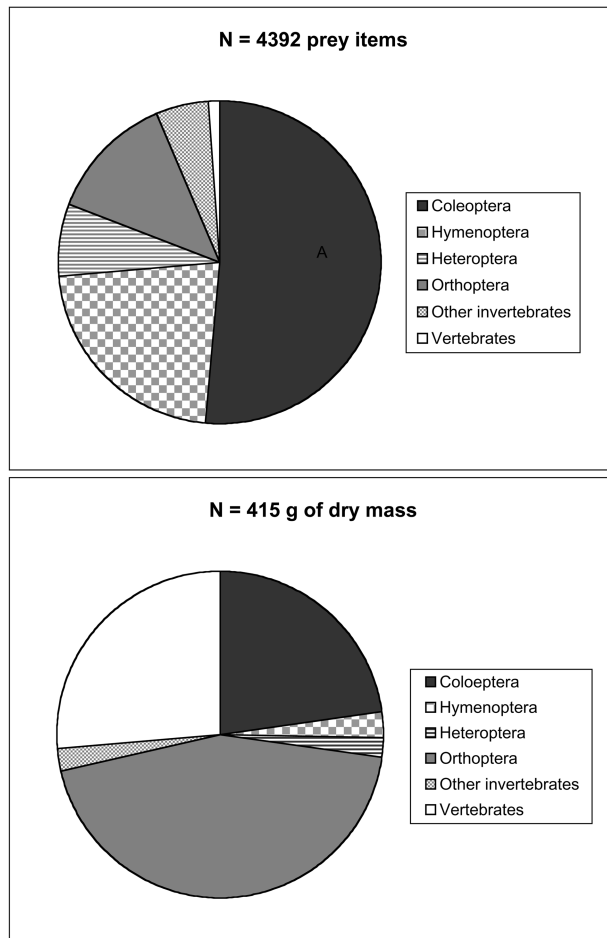


Fig. 2. – Density (top) and biomass (bottom) of potential invertebrate prey in territories of the red-backed shrike in Wielkopolska Province.

The red-backed shrike actual prey spectrum is significantly different from the potential one, both in terms of density of potential food ( $p < 0.001$ ) and its biomass ( $p <$

0.001). Out of five invertebrate taxa, Coleoptera, Hymenoptera and Orthoptera occurred in the content of red-backed shrike food more often than expected from sampling (“preferred food”), whereas Heteroptera and the category “other invertebrates” occurred less often (“avoided food”), both by numbers and by biomass (Table 2).

TABLE 2

The proportion of invertebrate groups in shrike territories and the proportion of prey selected by the red-backed shrikes in Wielkopolska Province, Poland. Explanations: PD – potential prey by density, PB – potential prey by biomass, SN – proportion among prey items in the red-backed shrike diet by number of specimens, SB – proportion of biomass given prey consumed. Index DD and Index DB – Ivlev’s selectivity index for numbering and biomass, respectively.

Prey items	PD	SN	Index		SB	Index DB
			DD	PB		
Coleoptera	0.265	0.615	0.632	0.182	0.420	0.530
Hymenoptera	0.030	0.218	0.799	0.010	0.073	0.775
Orthoptera	0.008	0.044	0.700	0.065	0.369	0.786
Heteroptera	0.418	0.077	-0.792	0.346	0.072	-0.744
Other invertebrates	0.279	0.046	-0.778	0.398	0.066	-0.807

## DISCUSSION

### Diet composition

The composition of the red-backed shrike diet is influenced by many external factors including habitat and territory quality, geographical location, weather conditions, time of day or season, as well as even by methods of food content analyses (CRAMP & PERRINS, 1993; HERNANDEZ et al., 1993; LEUGGER-EGGIMANN, 1997; TRYJANOWSKI et al., 2003).

The food composition of the red-backed shrike in Wielkopolska appears to be typical for its entire European range (review in: CRAMP & PERRINS, 1993). Especially large species of Coleoptera (Carabidae, Scarabeidae, Silphidae), Hymenoptera (*Apis*, *Vespa*, *Vespula*) and Orthoptera (*Tettigonia*) constituted a major part of the diet. Large species of beetles and orthopterans were found as the main red-backed shrike food in some areas (RANDIK, 1970; CRAMP & PERRINS, 1993; NIKOLOV, 2002). These prey can also be potential shrike population density regulators (KUPER et al., 2000). Moreover, it is possible to improve the quality of breeding territories by establishing special habitat patches for these insects (VAN NIEUWENHUYSE et al., 1999; KUPER et al., 2000). Both beetles and grasshoppers, are captured by relatively energetically non-expensive methods, known as the sit-and-wait strategy (LEFRANC & WORFOLK, 1997; VAN NIEUWENHUYSE et al., 1999). Our findings showed the red-backed shrike is ecologically flexible in using new food sources. For example, in the study area the cereal ground beetle *Zabrus tenebrioides* forms an important part of the red-backed shrike diet. Imago of the cereal ground beetles live on the ears of the cereals. On many occasions the red-backed shrikes were observed hovering over ears of the cereal crops, especially during plagues of these beetles in 2000, when density was up to 2 indiv. / 1m<sup>2</sup> (and biomass up to 175 mg / 1m<sup>2</sup>; J. KARG,

unpublished data). The shadow of birds causes beetles to roll off the plants as an antipredation reaction. They were then easily taken from the ground by the red-backed shrike.

As expected, the percentage of Hymenoptera in the diet (both by number and biomass) is high. However, as catching of bees and wasps is energetically costly (LEUGGER-EGGIMANN, 1997), these groups are probably less important for shrikes.

It is well known that vertebrates supplement the diet (LEFRANC & WORFOLK, 1997) and are represented by different taxa, i.e. small passerines, small mammals, lizards, frogs and even fish (KNYSH, 1982; HERNANDEZ, 1995). So far only MANSFELD (1958) tried to explain why red-backed shrike seldom caught vertebrates. He suggested that it depends on vertebrate availability. For example, during rich vole years they constituted up to 12% of prey items (and up to 87% by biomass). In many other studies, however, both during rich- and poor-vole years, vertebrates constituted only small percentages of the prey (e.g. LEFRANC & WORFOLK, 1997). We support the theory that red-backed shrike catch vertebrates so infrequently because attacking and handling time for this prey are energetically expensive (HERNANDEZ et al., 1993) while preying upon invertebrate appears to be a much less expensive hunting strategy. During cold and rainy weather, when insect activity is much reduced, red-backed shrikes are forced to prey on vertebrates.

### Prey preferences

Habitat selection in birds follows a sequential hierarchy (CODY 1985). While studying food preference within territories, we should remember that a previous step was territory site choosing. However, in this process the red-backed shrike can use information related to potential food sources and their availability (e.g. height of plant cover, number of perches, vegetation structure), and availability of safe nesting sites (KUŹNIAK & TRYJANOWSKI, 2000). The structure of potential food in the red-backed shrike territories is similar to the insect community in the whole farmland (KARG & RYSZKOWSKI, 1996). It is linked with insect richness in margin habitats (small woodlots, hedgerows, ecotones, small open patches with xerophilic plants) and meadows, both preferred by breeding red-backed shrikes (KUŹNIAK & TRYJANOWSKI, 2000).

Coleoptera, Hymenoptera and Orthoptera comprised preferred food of the red-backed shrike in the study area. In general, beetles were preferred, although these insects comprise a large and diverse group. It is well known that red-backed shrike prefer mostly large species (CRAMP & PERRINS, 1993; LEFRANC & WORFOLK, 1997), although they prey also upon small ones. Furthermore, among beetles we found species that secrete an odour, known as antipredator strategy (genus: *Silpha*, *Necrophorus*). Similarly, MIELEWCZYK (1976) found some individuals of the Colorado beetle *Leptinotarsa decemlineata* in the red-backed shrike diet. Other preferred groups, which use special antipredator strategies, were bees and wasps (Hymenoptera). The red-backed shrike efficiently caught these insects. Moreover, contrary to the suggestion by GWINNER (1961), bees sometimes are eaten, with their stings (often recorded in pellets).

In agreement with predictions (cf. VAN NIEUWENHUSE et al., 1999; KUPER et al., 2000) we found that Orthoptera

species were also an important part of the diet. On the other hand, in Spain, HERNANDEZ et al. (1993) indicated that grasshoppers and crickets are rather avoided, most probably due to local conditions.

### Recommendations for management

Detailed knowledge of the food consumed may assist management programs for the red-backed shrike (SCHIFFERLI et al., 1999; KUPER et al., 2000). We conclude that the red-backed shrike is very flexible in its use of different food spectra. Therefore, not only the food source in an agricultural landscape is a potential regulatory factor for the red-backed shrike population, but also prey accessibility. To improve red-backed shrike foraging success, places with short vegetation and additional perches should be prepared (VAN NIEUWENHUYSE et al., 1999). However, only management actions that focus on nest safety as well as foraging success can assist the red-backed shrike populations in modern farmland regions (LEFRANC, 1997; LEUGGER-EGGIMANN, 1997; SCHIFFERLI et al., 1999).

### ACKNOWLEDGEMENTS

We thank J. Kleban, M. Panigaj, M. Hromada and M. Antczak for their help in data collection. J. Bednorz, G. Kopij, J. Kosicki, M. Antczak and M. Hromada commented also on the first draft. C. Joiris and V. Takacs improved the manuscript prior publication.

### REFERENCES

- CODY, M.L. (ed.) (1985). *Habitat selection in birds*. Academic Press, San Diego, 558 pp.
- CRAMP, S. & C. M. PERRINS (eds.) (1993). *The Birds of the Western Palearctic. Vol. VII*. Oxford Univ. Press, Oxford, New York, 584 pp.
- HERNANDEZ, A. (1995). [Predation on amphibians, reptiles and birds by three shrike species *Lanius* spp. in northwestern Iberian Peninsula.] *Ecologia*, 9 : 409-415 (In Spanish).
- HERNANDEZ, A., F.J. PURROY & J.M. SALGADO (1993). [Seasonal variation, interspecific overlap, and diet selection in three sympatric shrike species (*Lanius* spp.).] *Ardeola*, 40 : 143-154. (In Spanish with English summary).
- JACOBS, I. (1974). Quantitative measurements of food selection: a modification of the forage ratio and Ivlev's Electivity index. *Oecologia*, 14 : 413-417.
- KARG, J. & L. RYSZKOWSKI (1996). Animals in arable land. In: RYSZKOWSKI, L., N.R. FRENCH, & A. KEDZIORA (eds.), *Dynamics of an agricultural landscape*. PWRiL, Poznań : 138-172.
- KNYSH, N.P. (1982). [Vertebrates in the diet of the Red-backed Shrike.] *Vestn. Zool.*, 8 : 84-86. (In Russian).
- KUPER, J., G.-J. VAN DUINEN, M. NIJSEN, M. GEERTSMA & H. ESSELINK (2000). Is the decline of the Red-backed Shrike (*Lanius collurio*) in the Dutch coastal dune area caused by a decrease in insect diversity? *Ring*, 22 : 11-25.
- KUŹNIAK, S. & P. TRYJANOWSKI (2000). Distribution and breeding habitat of the Red-backed Shrike (*Lanius collurio*) in an intensively used farmland. *Ring*, 22 : 89-93.
- LEFRANC, N. (1997). Shrikes and the farmed landscape in France. In: PAIN, D.J. & M.W. PIENKOWSKI (eds.), *Farming and birds in Europe*, Academic Press, London : 236-268.
- LEFRANC, N. & T. WORFOLK (1997). *Shrikes. A Guide to the Shrikes of the World*. Pica Press, Sussex, 192 pp.
- LEUGGER-EGGIMANN, U. (1997). *Parental expenditure of Red-backed Shrikes, *Lanius collurio*, in habitats of varying farm-*

- ing intensity. University of Basel & Swiss Ornithological Institute, Sempach, 103 pp.
- MANSFELD, K. (1958). Zur Ernährung des Rotrückenvürgers (*Lanius collurio collurio* L.), besonders hinsichtlich der Nestlingsnahrung, der Verteilung von Nutz- und Schadinsekten und seines Einflusses auf den Singvogelbestand. *Beitr. Vogelk.*, 6 : 271-292.
- MIELEWCZYK, S. (1967). On the food of the Red-backed Shrike, *Lanius collurio* L., near Gniezno (prov. of Poznań). *Acta orn.*, 10 : 157-175.
- NIKOLOV, B.P. (2002). Diet of the Red-backed Shrike *Lanius collurio* in Bulgaria. *Acrocephalus*, 23 : 21-26.
- RANDIK, A. (1970). [Red-backed Shrike (*Lanius collurio*) in natural conditions of Slovakia.] *Prace a studie SOP pri SUPSOP Bratislava*, 3 : 1-132. (In Slovak with English summary).
- ROSENBERG, K.V. & R.J. COOPER (1990). Approaches to avian diet analysis. *Stud. Avian Biol.*, 13 : 80-90.
- RYSZKOWSKI, L., N.R. FRENCH & A. KEDZIORA (1996). *Dynamics of an agricultural landscape*. PWRiL, Poznań, 223 pp.
- RYSZKOWSKI, L. & J. KARG (1977). Variability in biomass of epigeic insects in the agricultural landscape. *Ekol. Pol.*, 25 : 501-517.
- SCHIFFERLI, L., R.J. FULLER & M. MÜLLER (1999). Distribution and habitat use of bird species breeding on Swiss farmland in relation to agricultural intensification. *Vogelwelt*, 120, Suppl. : 151-161.
- TRYJANOWSKI, P., M.K. KARG & J. KARG (2003). Assessing shrike diet : comparing collars, pellets and prey remains in the Red-backed Shrike *Lanius collurio*. *Acta ornithologica* (37 : 67-72)
- TRYJANOWSKI, P. & S. KUŹNIAK (1999). Effect of research activity on the success of Red-backed Shrike *Lanius collurio* nests. *Ornis Fennica*, 76 : 41-43.
- TRYJANOWSKI, P., S. KUŹNIAK & B. DIEHL (2000). Breeding success of the Red-backed Shrike (*Lanius collurio*) in relation to nest site. *Ornis Fennica*, 77 : 137-141.
- TRYJANOWSKI, P. & T. SPARKS (2001). Is the detection of the first arrival date of migrating birds influenced by population size? A case study of the red-backed shrike *Lanius collurio*. *Int. J. Biometeorol.*, 45 : 217-219.
- VAN NIEUWENHUYSE, D., F. NOLLET & A. EVANS (1999). The ecology and conservation of the Red-backed Shrike *Lanius collurio* breeding in Europe. *Aves*, 36 : 179-192.
- ZAR, J.H. (1999). *Biostatistical analysis*. 4<sup>th</sup> Ed. Prentice Hall, New Jersey, 663 pp.

## APPENDIX

Diet composition of the red-backed shrike during the breeding season in Wielkopolska Province, Poland. N denotes number of prey items (in number of individuals), whereas Prey is ratio of the total prey number, Bio is ratio of biomass (in mg of dry mass) consumed.

Prey item	N	Prey	Biomass	Bio
Coleoptera	2261	0.515	95072	0.229
Carabidae	1091	0.248	72323	0.174
<i>Carabus violaceus</i>	4	0.001	535	0.001
<i>Carabus cancelatus</i>	1	0.000	126	0.000
<i>Carabus</i> sp.	69	0.016	9225	0.022
Carabidae indet.	5	0.001	118	0.000
<i>Broscus cephalotes</i>	1	0.000	54	0.000
<i>Bembidion</i> sp.	70	0.016	82	0.000
<i>Agonum</i> sp.	5	0.001	42	0.000
<i>Lebia</i> sp.	1	0.000	26	0.000
<i>Calosoma</i> sp.	49	0.011	12332	0.030
<i>Amara</i> sp.	89	0.020	756	0.002
<i>Calathus</i> sp.	95	0.022	1617	0.004
<i>Harpalus</i> sp.	2	0.000	52	0.000
<i>Idiochroma</i> sp.	1	0.000	5	0.000
<i>Ophonus</i> sp.	14	0.003	119	0.000
<i>Pterostichus</i> sp.	397	0.090	21512	0.052
<i>Pterostichus cupreus</i>	1	0.000	54	0.000
<i>Zabrus tenebrioides</i>	287	0.065	25666	0.062
Scarabaeidae	719	0.164	7485	0.018
<i>Anomala dubia</i>	571	0.130	3023	0.007
<i>Anomala aenea</i>	1	0.000	42	0.000
<i>Aphodius fimetarius</i>	16	0.004	143	0.000
<i>Aphodius rufus</i>	1	0.000	9	0.000
<i>Aphodius fossor</i>	1	0.000	9	0.000
<i>Aphodius</i> sp.	15	0.003	101	0.000
<i>Rhizotroous</i> sp.	7	0.002	556	0.001
<i>Onthophagus</i> sp.	5	0.001	48	0.000
<i>Valgus hemipterus</i>	1	0.000	21	0.000
<i>Geotrupes stercorosus</i>	1	0.000	92	0.000
<i>Geotrupes</i> sp.	23	0.005	2105	0.005
<i>Phyllopertha horticola</i>	77	0.018	1336	0.003
Curculionidae	159	0.036	1083	0.003
<i>Phyllobius</i> sp.	82	0.019	300	0.001
<i>Cleonus</i> sp.	1	0.000	1	0.000
<i>Otiorrhynchus</i> sp.	16	0.004	596	0.001
<i>Sitona</i> sp.	17	0.004	79	0.000
Curculionidae indet.	43	0.010	107	0.000

Prey item	N	Prey	Biomass	Bio
Elateridae	59	0.013	810	0.002
<i>Selatosomus aeneus</i>	5	0.001	176	0.000
<i>Agriotes</i> sp.	27	0.006	261	0.001
Elateridae indet.	27	0.006	373	0.001
Staphylinidae	84	0.019	483	0.001
<i>Lathrobium</i> sp.	1	0.000	2	0.000
<i>Ontholestes</i> sp.	14	0.003	226	0.001
<i>Philonthus</i> sp.	46	0.010	66	0.000
<i>Staphylinus</i> sp.	5	0.001	164	0.000
<i>Heterothops</i> sp.	4	0.001	1	0.000
Staphylinidae indet.	14	0.003	25	0.000
Silphidae	63	0.014	10752	0.026
<i>Nicrophorus</i> sp.	32	0.007	8507	0.020
<i>Silpha sinuata</i>	1	0.000	26	0.000
<i>Silpha</i> sp.	18	0.004	468	0.001
Silphidae indet.	12	0.003	1751	0.004
Chrysomelidae	17	0.004	176	0.000
<i>Lema</i> sp.	3	0.001	9	0.000
<i>Leptinotarsa decemlineata</i>	1	0.000	74	0.000
Chrysomelidae indet.	13	0.003	93	0.000
Histeridae	12	0.003	84	0.000
<i>Hister</i> sp.	12	0.003	84	0.000
Cerambycidae	10	0.002	479	0.001
<i>Spondylis buprestoides</i>	2	0.000	17	0.000
<i>Saperda</i> sp.	1	0.000	58	0.000
Cerambycidae indet.	7	0.002	404	0.001
Leioididae	3	0.001	0	0.000
<i>Anisotoma humeralis</i>	3	0.001	0	0.000
Cicindellidae	2	0.000	17	0.000
<i>Cicindela</i> sp.	1	0.000	8	0.000
<i>Cicindela campestris</i>	1	0.000	8	0.000
Lagriidae	3	0.001	112	0.000
<i>Lagria hirta</i>	3	0.001	112	0.000
Nitidulidae	4	0.001	2	0.000
<i>Meligethes</i> sp.	4	0.001	1	0.000
Others Coleoptera	37	0.008	1266	0.003

Prey item	N	Prey	Biomass	Bio
Hymenoptera	971	0.221	9872	0.024
Formicidae	291	0.066	258	0.001
<i>Formica rufa</i>	56	0.013	66	0.000
<i>Lasius niger</i>	145	0.033	91	0.000
<i>Lasius</i> sp.	7	0.002	4	0.000
<i>Formica</i> sp.	83	0.019	95	0.000
Ichneumonidae	328	0.075	992	0.002
<i>Ophion</i> sp.	31	0.007	247	0.001
<i>Ophion luteus</i>	3	0.001	24	0.000
Cryptinae	24	0.005	59	0.000
Ichneumonidae indet.	270	0.061	662	0.002
Apidae	157	0.036	3933	0.009
<i>Apis mellifera</i>	66	0.015	1416	0.003
<i>Apis</i> sp.	5	0.001	107	0.000
<i>Andrena</i> sp.	13	0.003	114	0.000
<i>Bombus</i> sp.	28	0.006	1420	0.003
<i>Nomada</i> sp.	1	0.000	4	0.000
Apidae indet.	44	0.010	872	0.002
Vespidae	153	0.035	3937	0.009
<i>Vespa rufa</i>	20	0.005	515	0.001
<i>Vespa vulgaris</i>	2	0.000	51	0.000
<i>Vespa germanica</i>	41	0.009	1055	0.003
<i>Vespa</i> sp.	75	0.017	1930	0.005
<i>Vespa crabro</i>	5	0.001	129	0.000
<i>Vespa</i> sp.	8	0.002	643	0.002
<i>Dolichovespula norvegica</i>	1	0.000	26	0.000
<i>Dolichovespula sylvestris</i>	6	0.001	154	0.000
Vespidae indet.	2	0.000	51	0.000
Myrmicidae	19	0.004	22	0.000
<i>Myrmica</i> sp.	19	0.004	22	0.000
Eumenidae	9	0.002	44	0.000
Sphecidae	3	0.001	50	0.000
<i>Ammophila sabulosa</i>	2	0.000	43	0.000
Sphecidae indet.	1	0.000	7	0.000
Mutillidae	1	0.000	2	0.000
Aryidae	1	0.000	2	0.000
Tenthredinidae	1	0.000	10	0.000
Chrysididae	1	0.000	3	0.000
Heteroptera	317	0.072	7823	0.019
Pentatomidae	286	0.065	7661	0.018
<i>Palomena prasina</i>	30	0.007	697	0.002
<i>Palomena</i> sp.	3	0.001	70	0.000
<i>Pentatoma</i> sp.	3	0.001	98	0.000
<i>Picromerus bidens</i>	2	0.000	65	0.000
<i>Eurygaster maura</i>	53	0.012	1922	0.005
<i>Eurygaster</i> sp.	6	0.001	218	0.001
<i>Eurydema oleracea</i>	2	0.000	16	0.000
<i>Dolycoris</i> sp.	7	0.002	81	0.000
<i>Aelia acuminata</i>	14	0.003	200	0.000
<i>Aelia</i> sp.	4	0.001	57	0.000
Pentatomidae indet.	162	0.037	4237	0.010
Lygaeidae	3	0.001	4	0.000
Acanthosomidae	2	0.000	16	0.000
Miridae	5	0.001	11	0.000
<i>Notostira</i> sp.	2	0.000	5	0.000
<i>Lygus</i> sp.	3	0.001	6	0.000
Coreidae	3	0.001	96	0.000
<i>Coreus</i> sp.	2	0.000	74	0.000
Coreidae indet.	1	0.000	22	0.000
Nabidae	16	0.004	32	0.000
<i>Nabis ferus</i>	3	0.001	6	0.000

Prey item	N	Prey	Biomass	Bio
<i>Nabis</i> sp.	13	0.003	26	0.000
Tingidae	1	0.000	0	0.000
<i>Tingis</i> sp.	1	0.000	0	0.000
Berytidae	1	0.000	1	0.000
<i>Berytinus</i> sp.	1	0.000	1	0.000
Orthoptera	568	0.129	183206	0.441
Tettigonidae	455	0.104	178211	0.429
<i>Tettigonia</i> sp.	434	0.099	177940	0.429
<i>Metrioptera roselli</i>	1	0.000	119	0.000
Tettigonidae indet.	10	0.002	152	0.000
Acridiidae	122	0.028	4955	0.012
<i>Chorthippus</i> sp.	30	0.007	1218	0.003
Acridiidae indet.	92	0.021	3736	0.009
Orthoptera indet.	1	0.000	41	0.000
Dermaptera	25	0.006	293	0.001
Forficulidae	25	0.006	293	0.001
<i>Forficula auricularia</i>	12	0.003	141	0.000
<i>Chelidurella acanthopygia</i>	1	0.000	12	0.000
<i>Forficula</i> sp.	2	0.000	23	0.000
Forficulidae indet.	10	0.002	117	0.000
Blattodea	1	0.000	2	0.000
Blattidae	1	0.000	2	0.000
<i>Ectobius</i> sp.	1	0.000	2	0.000
Odonata	10	0.002	5535	0.013
Diptera	87	0.020	805	0.002
Sarcophagidae	19	0.004	269	0.001
Calliphoridae	21	0.005	297	0.001
<i>Lucilia</i> sp.	1	0.000	14	0.000
Calliphoridae indet.	20	0.005	283	0.001
Tachinidae	12	0.003	286	0.001
<i>Tachina</i> sp.	1	0.000	3	0.000
Tachinidae indet.	8	0.002	27	0.000
Muscidae	2	0.000	12	0.000
Bibionidae	10	0.002	13	0.000
Asillidae	4	0.001	56	0.000
Diptera indet.	22	0.005	128	0.000
Lepidoptera	39	0.009	335	0.001
Noctuidae	3	0.001	24	0.000
<i>Agrotis</i> sp.	3	0.001	24	0.000
Lepidoptera larvae indet.	34	0.008	305	0.001
Lepidoptera indet.	2	0.000	5	0.000
Neuroptera	2	0.000	6	0.000
Myrmeleontidae	1	0.000	3	0.000
<i>Myrmeleon</i> sp.	1	0.000	3	0.000
Chrysopidae	1	0.000	3	0.000
Homoptera	4	0.001	14	0.000
Cercopidae	3	0.001	13	0.000
<i>Philaenus</i> sp.	3	0.001	13	0.000
Iassidae	1	0.000	1	0.000
<i>Aphrodes</i> sp.	1	0.000	1	0.000
Diplopoda	27	0.006	1804	0.004
Isopoda	9	0.002	192	0.000
Araneae	5	0.001	14	0.000
Opiliones	2	0.000	5	0.000
Molusca	12	0.003	6	0.000
<b>Invertebrates total</b>	<b>4343</b>	<b>0.989</b>	<b>304998</b>	<b>0.735</b>
Aves	3	0.001	18000	0.043
Mammalia	46	0.010	12000	0.029
<b>Vertebrates total</b>	<b>49</b>	<b>0.011</b>	<b>110000</b>	<b>0.265</b>

Received: December 19, 2002

Accepted: April 10, 2003