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Variable contribution of functional prey groups in diets reveals inter- and intraspecific differences in faecal concentrations of essential and non-essential elements in three sympatric avian aerial insectivores: A re-assessment of usefulness of bird faeces in metal biomonitoring

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ABSTRACT

Aerial insectivores through their insect diet can contribute to biotransfer of elements across habitats. We investigate the relationship between dietary composition as expressed by the contributions of six functional invertebrate prey groups (primarily of agriculturally subsidised invertebrates characteristic of agricultural areas in temperate regions of Europe) and concentrations of essential (Na, K, Ca, Mg, Fe, Cu, Zn, Mn, Co) and non-essential (As, Cd, Pb) elements of environmental concern in the faeces of nestlings of three species of avian aerial insectivores – Common Swift *Apus apus*, Barn Swallow *Hirundo rustica* and House Martin *Delichon urbicum* – which breed sympatrically and use apparently similar resources of flying insect prey. There were significant differences between the species for 7 of the 12 elements (Ca, Zn, Cu, Co, As, Pb, Cd); these differences were attributable to the variable dietary composition, even though the concentrations of the elements varied enormously between the faecal samples from the individual species. Partial correlation analysis between the biomass (expressed in mg dry weight) of the six functional prey groups and faecal concentrations of elements showed the highest number of significant relationships for toxic metals (As, Pb and Cd). The results of the General Regression Model explaining faecal element concentrations revealed the different explanatory power of the effects of PCA (of six functional prey groups) dietary scores. A significant fit of GRM was obtained for 7 elements (Na, Mg, Fe, Mn, As, Pb, Cd) for Barn Swallows, 2 elements (Cu, As) for House Martins and 1 element (Mn) for Common Swifts. Overall, the results confirmed our predictions that the biomass of consumed coprophilous taxa and insects from crop habitats was positively correlated with the faecal concentrations of toxic elements. Unexpectedly, however, the faecal samples (primarily those of Common Swifts) that contained many oil-seed rape insect pests had lower Ca, Pb and Cd levels and a higher As level. Our study implies that the cross-boundary transfer of contaminants, primarily non-essential elements, by aerially foraging birds through the considerable accumulation of their faeces has potential consequences for the local biogeochemical cycle and environmental quality.

1. Introduction

Invertebrates, including insects, make up a substantial part of the terrestrial food web, since they are a staple component of the diets of a variety of animals from higher trophic levels. Invertebrates can accumulate in their bodies (both in subcellular structures and/or along with the ingested food contained in their digestive systems) various chemical elements or substances, including anthropogenic contaminants of the environment like trace metals or pesticides. Knowledge of the biotransfer and/or assimilation of elements/contaminants at different levels of this food chain can provide key insight into their flow and ecological energy regimes (Hunter et al., 1987; Vermeulen et al., 2009; Schipper et al., 2012; Kraus et al., 2014). Importantly, the flow of elements often runs between different ecosystems (e.g. from aquatic/marine to terrestrial) (Paetzold et al., 2005; Yin et al., 2008; Alberts et al., 2013; Signa et al., 2013; Kraus et al., 2014) or between various habitats within the same terrestrial ecosystem (e.g. crop fields–non-crop areas) (Vermeulen et al., 2009; Schipper et al., 2012). The latter case of cross-boundary biotransfer of elements or contaminants in

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agricultural areas is especially important, since the flow of agricultural chemicals used to increase yields is nowadays a problem that goes beyond intensively farmed areas (Alberts et al., 2013; Signa et al., 2013; Kraus et al., 2014).

In general, both invertebrates and vertebrates excrete the majority or excess of consumed essential and non-essential elements through the faeces (Vijver et al., 2004; Yin et al., 2008; Ding et al., 2013). Nestling birds can eliminate through the faeces about 92% of Cd and 85% of Pb from the entire content of these metals supplied (Świergosz et al., 1998; reviewed in Martínez-Haro et al., 2010). Consequently, faeces can be a sensitive indicator of environmental contamination by metals and their availability in the food items of higher-trophic consumers, such as insectivorous birds (Spahn and Sherry, 1999; Dauwe et al., 2000, 2004; Morrissey et al., 2004; Yin et al., 2008; Berglund et al., 2010; Costa et al., 2012). One benefit of the use of faeces, apart from its being a non-destructive and non-invasive sampling technique, is that they generally contain high concentrations of metals, often higher than the food items themselves, which makes for easy quantification (Morrissey et al., 2004). To some extent, therefore, faeces are useful as an indicator of the potential accumulation of As, Cd and Pb also in internal tissues; more importantly, however, they signal an increased risk of physiological stress resulting from the expenditure of resources on excreting excess metals from the body (Berglund et al., 2010). Even though a number of studies have reported on concentrations of essential and non-essential elements in avian excreta, most of them do not relate the levels of elements to dietary composition: they merely state the concentration of individual elements or compare the elemental content between two or more areas, often referred to a priori as polluted and control areas (e.g. Leonzio et al., 2009; Costa et al., 2012; Dauwe et al., 2004; Eeva and Lehikoinen, 2004). Therefore, a detailed examination of the potential relationship between dietary variation (spatially and temporally highly variable in most species of insectivorous birds) and faecal element concentrations cannot be carried out in such a simplified way. In this context, an exception are studies where attempts have been made to explore the relationship between variation in diet and faecal metal concentrations, as in the case of two forest insectivorous passerines, the Great Tit *Parus major* and Pied Flycatcher *Ficedula hypoleuca*, from polluted and control areas of SW Finland (Eeva et al., 2005; Berglund et al., 2010). Furthermore, since during the year metal contamination levels vary significantly (Hunter et al., 1987) between invertebrate groups and trophic levels (e.g. detritivores show the greatest single stepwise increase in Cd concentration in the food chain), one should expect that the concentrations of elements in the faeces of insectivorous birds (and other predator species depending on seasonally or spatially/geographically separate food resources) will be equally variable.

The impacts of anthropogenic encroachment into aerial habitats are not well understood. Insectivorous birds and bats are inherently valuable components of biodiversity and play an integral role in aerial trophic dynamics (Kelly et al., 2013). In the context of the local accumulation of contaminants (e.g. from sewage/waste effluent) transferred through the food web or higher-trophic consumers like aerially foraging vertebrate insectivores, which are important predators of flying insects and provide biological control of insect pests in agricultural systems, where chemical control or fertilisation is commonly used (Nocera et al., 2012; Alberts et al., 2013; Kelly et al., 2013). Aerial insectivores are especially likely to bioaccumulate a high content of toxic metals and other contaminants through their insect diet taken in areas where pollution levels are high (Grue et al., 1984; Kraus, 1989; Kamiński et al., 1993a,b; Wayland et al., 1998; McCarty, 2001; Alberts et al., 2013; Gilchrist et al., 2014; Cruz-Martinez et al., 2015). It should be remembered, moreover, that some bats and aerially foraging birds are synanthropic and during their reproductive season operate over relatively small distances from their breeding sites, which are located primarily in buildings within human settlements (Turner, 2006; Nocera et al., 2012). This implies that in circumstances where large volumes of faeces have aggregated over many decades or even centuries, aerial foragers can contribute to the biotransfer of contaminants from crop fields to areas inhabited by people (e.g. Nocera et al., 2012). The present scarcity of data relating the dietary data and accumulation of elements in avian faeces clearly points to the need for such a detailed analysis, which is an important contribution to knowledge of ecosystem functioning and the cross-boundary transfer of energy and contaminants (Nocera et al., 2012; Alberts et al., 2013; Kelly et al., 2013).

The present study addresses the above issues by investigating the relationship between dietary composition, expressed as the contribution of functional invertebrate prey groups characteristic of agricultural areas in temperate regions of Europe, and the concentrations of minerals (Na, K, Ca, Mg, Fe, Cu, Zn, Mn, Co) and toxic metals of environmental concern (As, Cd, Pb) determined in faeces of three avian aerial insectivore species, the Common Swift *Apus apus*, Barn Swallow *Hirundo rustica* and House Martin *Delichon urbicum*. These birds breed sympatrically and use apparently similar resources of flying insect prey, primarily of agriculturally subsidised invertebrates. As the community of flying insects consists of a great many different taxa, we used in the present study our previous classification of invertebrates identified in the diets of these three bird species into six consistent functional groups of prey with respect to their habitat, food or association with crop habitat (Orłowski et al., 2014a). Overall, our classification of flying insects concurs with some previous concepts of functional biodiversity within agricultural landscapes (Tscharntke et al., 2005; Moonen and Bàrberi, 2008; Fahrig et al., 2011). Similar approaches of functional traits of invertebrates were recently applied to an assessment of soil pollution, and the development of these methods based on multiple expertise information or features of a species is desirable (Hedde et al., 2012). Specifically, in the present study we test the hypothesis that some prey groups, such as coprophilous (including saprophagous) insect taxa (preyed primarily by Barn Swallows and House Martins), which are especially liable to bioaccumulate high levels of toxic elements by consuming the excrement of farm animals (primarily from manure with extremely high Cd, Cu and Zn levels derived from food additives) or soil (Hunter et al., 1987; de Vries et al., 2002; Dach and Starmans, 2005; Hedde et al., 2012), may elevate the concentrations of these elements in the faeces of aerial insectivores. In turn, since phytophagous insects, such as pests of oil-seed rape and other arable crops (preyed primarily by Common Swifts), are treated with insecticides or other agrochemicals, we anticipated a higher content of some trace elements (e.g. As) in faecal samples, which contained proportionately large numbers of these insects. The opposite relation may be associated with the presence in the diet of insects living in non-crop habitats, where agrochemicals are not applied (these prey types are consumed by three studied aerial insectivores with variable intensity over the breeding season), which could imply a lower content of toxic elements. An equally important question addressed in our study is how dietary composition is related to the faecal concentrations of minerals in three studied species, which are crucial factors for the normal growth of nestlings and the successful breeding of birds (Blancher and McNicol, 1988; Graveland and van Gijzen, 1994; Scheuhammer et al., 1997; Eeva and Lehikoinen, 2004). Determining the levels of both these groups of elements may be crucial in the search for an explanation of potential differences between the target birds. The question of minerals, mainly Ca, is especially important in the ecophysiology of aerially foraging birds, since some previous studies have shown that insects are not a sufficient source of Ca for shell formation and the skeletal growth of nestlings (Blancher and McNicol, 1988; Graveland and van Gijzen, 1994; Scheuhammer et al., 1997). To the best of our knowledge, minerals apart from Ca have rarely been analysed in the faeces of insectivorous birds; hence the lack of reliable data on their faecal levels. Furthermore, considering that aerially foraging birds feed exclusively in the air – the Common Swift in particular is an extreme case of morphological adaptation to flight and feeding in the upper air layers compared with the other two target species and never take food items or grit from the ground (Waugh, 1978; Cramp, 1998) – we expected that this species would exhibit considerable mineral shortages, as indicated by low faecal levels.

2. Material and methods

2.1. Study area and species and faeces collection

In the analysis of the elemental content of faeces we used a series of faecal sacs from nestlings of Common Swifts, House Martins and Barn Swallows selected from a larger number of samples examined in our previous dietary studies conducted over two entire breeding seasons (June–September) in 2011 and 2012, at Stary Gołębin (Orłowski and Karg, 2013a; Orłowski et al., 2014a), a village in an agricultural region of western Wielkopolska (SW Poland). This area is characterised by intensive agricultural production of both arable crops and livestock (see more details in Orłowski et al., 2014a; see Supplementary data S1). All crops within a 500 m radius were managed (over several years) using conventional amounts of agrochemicals, including pesticides and fertilisers. The land holder (Top Farms Wielkopolska Co., Poland) supplied management data on agricultural practices, including pesticide application on individual fields for the study years — 2010/2011 and 2011/2012. The fields of winter oil-seed rape (cultivar: Vision and PRW 31 F-1) were sown between 20 and 25 September 2010 and 2011; in spring there were 2 herbicide, 10/6 fungicide and 3/5 insecticide applications between March and May (in 2010/2011 and 2011/2012 respectively) targeting stem weevils *Ceutorhynchus* spp. and pollen beetles *Meligethes* spp. The crop was harvested between 15 and 20 July. In 2011 the maize crops were treated 3–4 times with herbicide, 0–3 times with fungicide and 0–1 time with insecticide; they were harvested in October. In 2011 two fields of winter wheat were treated 2–3 times with herbicide, 4 times with fungicide and once with insecticide. In addition, most arable crops were treated up to three times in spring with a mixture of trace elements (Mg, Bo, Mn, Cu, Zn, Mo), growth regulators and organic fertilisers (manure and slurry).

2.2. Determination of diet and functional prey groups

Overall, the elemental analysis used faecal sacs selected uniformly from a large number of samples obtained in 2011 and 2012; a total of 57 (38/19 from 2011/2012) faecal sacs from Common Swifts, 66 (39/27) from Barn Swallows and 60 (40/20) from House Martins were analysed. In the further analysis all these selected faecal sacs were treated as independent units (see Supplementary data S1 on more details on the faecal sac collection). The method of faecal analysis is presented elsewhere in detail (Orłowski and Karg, 2011, 2013a,b). Briefly, initially, we identified invertebrate prey items to the lowest possible taxonomic level in all individual faecal sacs (see Supplementary data S1). The mass of prey has been expressed as calculated for dry mass, i.e. mg d.w.; these values were obtained from detailed measurements of insect weights based on analysis of 479,087 individuals of different taxa of insects (Karg, 1989). Overall, analysis of faeces is likely to yield a reliable picture of the diet of aerial insectivores, since earlier findings of the experimental feeding of a nestling Barn Swallow conducted by Waugh (1978) showed that the proportions of different prey types ingested (including some soft-bodied prey types such as small Diptera) and the proportions recovered in the faeces are in very close agreement. This essentially means that no significant differential digestion exists between prey types with soft bodies and flexible wings and heavily chitinised prey (Waugh, 1978). In addition, the results of our previous field studies on insect fauna in various crop types and non-crop habitats situated in a neighbouring farming area did not indicate that any major insect group was missing from the faecal samples, which might have been expected based on these collections (Orłowski et al., 2014a).

Owing to the highly aggregated, taxonomically diverse invertebrate community in an agricultural landscape (e.g. Ryszkowski et al., 1993; Tscharntke et al., 2005; Schweiger et al., 2005; Bengtsson et al., 2005) we expressed the dietary composition of the aerial insectivores as the contributions of functional invertebrate prey groups theoretically formulated and applied in our previous dietary study of the community of these three species (Orłowski et al., 2014a). This classification is based firstly on the relationship of insect species with the type of vegetation that they inhabit, secondly on the agricultural activities that provide the habitat for their development and their association with crop or non-crop habitats, and finally on the ecological services provided to agriculture by the individual prey species. All the identified prey taxa were classified into six functional invertebrate groups: 1) oil-seed rape pests; 2) pests of other arable crops, i.e. feeding/developing in broad-leaved crops, cereals, vegetables and lucerne cultivation; 3) other crop-provisioned invertebrate taxa (various invertebrates, including predatory insects living in crop habitats); 4) coprophilous/coprophagous insects (such as dung/manure-feeding beetles and some large dipterans; hereafter referred to as 'coprophilous taxa'); 5) invertebrates from non-crop habitats (various food guilds associated with woodland/permanent vegetation); and 6) invertebrates from mixed crop/non-crop habitats (occurring in both these habitats). With the exception of the group of invertebrates from non-crop habitats, all the functional invertebrate groups can be formally pooled into invertebrate resources that are agriculturally subsidised, i.e. exhibit some dependence on agricultural activities. A detailed list of all identified prey taxa is given elsewhere (Orłowski and Karg, 2013a; Orłowski et al., 2014a).

2.3. Chemical analysis

For chemical analysis we used the entire faecal sacs weighing 100–210 mg, collected under active nests of the three studied species. Samples were placed in tightly sealed neutral polyethylene boxes. Overall, we analysed 57, 66 and 60 faecal sacs from nestlings of Common Swifts, Barn Swallows and House Martins, respectively. The majority of faecal sacs were sampled from paper sheets placed under active nests or concrete floors (not in contact with the soil) sampled in various parts of the colony, so the faeces very likely came from several different broods. In the elemental content analysis we used material from faecal sacs that had been manually crushed during prey identification — prior to this treatment all external materials, like feathers or sand particles, were removed. The material to be analysed thus contained various undigested chitin remains of insects and loose grains of faeces containing highly digested food residues. The samples for chemical analysis were weighed and dried to constant dry mass at a temperature of 65 °C. For the analysis of 12 elements, including 9 essential ones (Na, K, Ca, Mg, Fe, Cu, Zn, Mn, Co) and 3 toxic ones (As, Cd, Pb), we used the entire faecal sacs weighing 100–210 mg. Samples were then homogenised with a porcelain pestle and mortar. The analyses were done on a Perkin-Elmer atomic absorption spectrophotometer (AAS) (Analyst 800-RW0683/3PYC) (Weltz, 1985; see more details, including quality control in Supplementary data S2).

2.4. Data analysis

Our primary goal was to determine the extent to which differences in dietary composition (calculated for the one individual faecal sac), expressed as the number (real number of invertebrate prey), biomass (absolute biomass of prey in mg dry weight; mg d.w.) and proportional dietary biomass (% biomass) of six functional invertebrate prey groups among Common Swifts, Barn Swallows and House Martins, were indicative of the faecal levels of minerals and toxic metals and which functional prey groups affected the recorded elemental concentrations.

Initially, we used MANOVA to assess the differences in the number, biomass (mg d.w.) and percentage biomass of the six functional prey groups in the individual faecal sacs from the three target species. A *post-hoc* comparison (LSD test) was later applied to reveal in detail how the contributions of the prey groups varied between the three species. Prior to MANOVA, some dietary variables and elemental concentrations were log-transformed to comply with the assumptions of normality, and percentage data were square-root transformed. Since the number of prey merely tells us about the dietary composition and not about the volume or amount of ingested food/elements, we used the biomass of prey (i.e. total dry mass of the six functional prey groups per one faecal sac) as potential correlates with elemental concentrations in all our analyses.

In view of the multivariate nature of dietary data, we used Principal Component Analysis (PCA) to group the biomasses (expressed in mg dry weight) of the six functional prey groups into consistent independent variables. We performed four PCAs using Statistica 7.0 (StatSoft, 2006) on standardised log-transformed biomasses across the three species pooled, and for each species individually. In PCA we applied varimax normalised factor rotation. Factor loadings were used to interpret PC patterns across different species. Principal components (PCs) with an eigenvalue > 1 were assumed to account for a significant contribution to the total variance according to the latent root criterion (Hair et al., 1998).

We assessed the effect of the biomass of the six functional prey groups on elemental concentrations in faeces in two ways. The first was a univariate approach using partial correlation analysis (StatSoft, 2006). This analysis was performed simultaneously for the entire set of biomasses of the six functional prey groups and the concentration of a given element; the remaining correlates acted as controls. In general, due to low number of significant relationships obtained in this analysis (presented as Supplementary data S3 and S4) we report p-values directly, leaving readers the possibility of the further evaluation of the accuracy of these results. The second way was a multivariate approach using the General Regression Model (GRM) (StatSoft, 2006). In GRM, separate models were constructed for the concentration of each element (on log-transformed data) and the effect (β-values) of dietary principal components was tested. F-values and R^2 are given as the final result of GRM.

The statistical analyses were done with Statistica 7.0 (StatSoft, 2006). A probability of $p < 0.05$ was assumed to be statistically significant.

3. Results

3.1. Dietary composition and species-specific dietary differences between the three sympatric avian aerial insectivores

Overall, MANOVA revealed marked differences in dietary composition expressed by the six major functional prey groups identified in the entire set of faecal sacs among Common Swifts, Barn Swallows and House Martins: number of prey (Wilks's Lambda, $\lambda_{12,350} = 0.406$, $p < 0.0001$; Fig. 1a), biomass of prey (Wilks's Lambda, $\lambda_{12,350} = 0.408$, $p < 0.0001$; Fig. 1b) and percentage biomass of prey (Wilks's Lambda, $\lambda_{12,350} = 0.428$, $p < 0.0001$; Fig. 1c). The diet composition expressing the biomasses (mg d.w.) of six major functional prey groups in the faecal sacs of the three target species varied enormously and exhibited a wide variability attributable to day-to-day, seasonal and/or even year-to-year differences (see Supplementary data S3).

PCA of the six functional prey groups identified in the faecal sacs consistently yielded three components with eigenvalues within a relatively small range from 1.10 to 1.54 across all three pooled and individual aerial insectivore species (Table 1). Overall, the PCA results explained from 18% to 26% of the variance, even though there were slight differences in the grouping of some prey groups and the direction of their association (Table 1). For Common Swifts, the PC1 scores of insects of crop habitats and coprophilous taxa were loaded in a positive direction; insects from mixed and non-crop habitats were loaded as PC2 in a positive and a negative direction respectively; only oil-seed rape pests were loaded as PC3 in a negative direction. For Barn Swallows, the PC1 scores of other pests and insects from non-crop habitats were loaded; insects from crop habitats and coprophilous taxa were loaded as PC2; and oil-seed rape pests were loaded as PC3; all these associations were in a positive direction. Similarly, for House Martins only a positive direction of associations was observed: insects from crop and non-crop habitats were loaded as PC1, insects from mixed habitats and oil-seed rape insect pests were loaded as PC2, and coprophilous taxa were loaded as PC3 (Table 1).

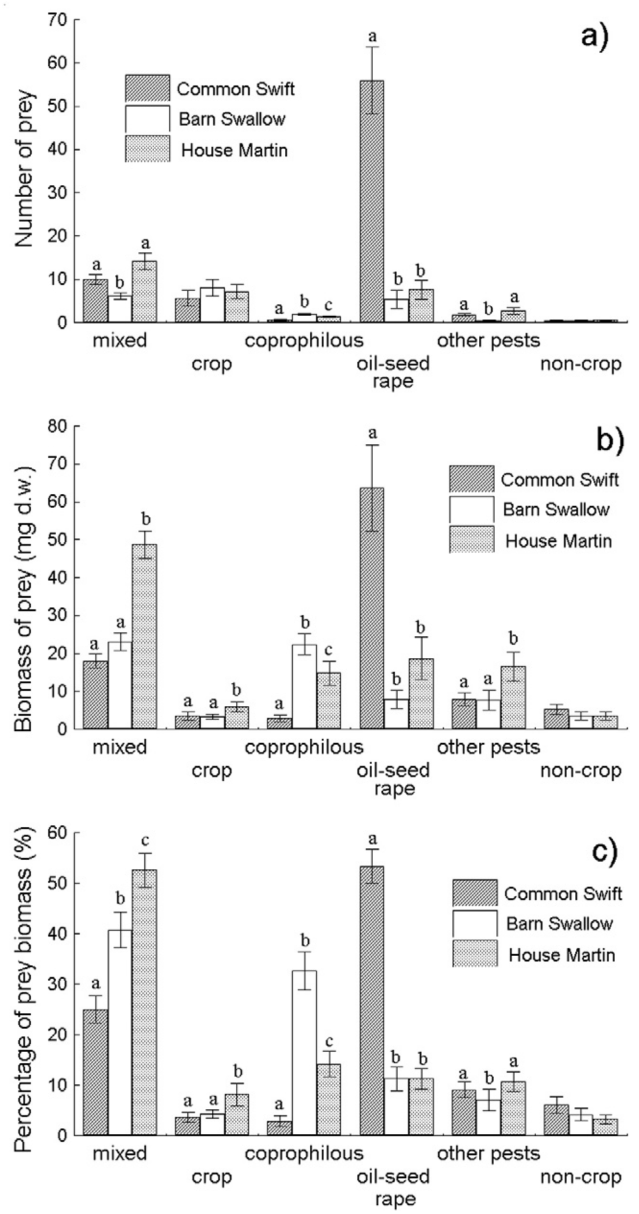

Fig. 1. Dietary composition of nestlings of three sympatric aerial insectivorous feeding birds in south-west Poland expressed as the average (± SE) number (a), biomass (b) and percentage biomass (c) of six functional prey groups identified in individual faecal sacs from Common Swifts ($n = 57$), Barn Swallows ($n = 66$) and House Martins ($n = 60$); samples sharing a letter or without any letter are not significantly different in the *post-hoc* comparison.

3.2. Essential and non-essential elements in faeces: sources of variation and dietary dependence

Overall, seven of the twelve elements analysed in faeces showed significant differences among the three target bird species: four essential

Table 1
Component values and factor loadings of the Principal Component Analysis (PCA) of the biomass (mg d.w.) of six functional prey groups (*see* Fig. 1) identified in individual faecal sacs of three sympatric aerial insectivorous feeding birds; factor rotation: varimax normalised; the figures in bold indicate the variable for which each factor exhibited the greatest variability.

Prey group	Axis		
	PC1	PC2	PC3
Common Swift			
Mixed	0.297	**0.703**	0.354
Crop	**0.787**	0.043	−0.222
Coprophilous	**0.859**	−0.110	0.110
Oil-seed rape	0.092	0.114	**−0.871**
Other pests	0.006	−0.225	−0.413
Non-crop	0.287	**−0.839**	0.101
Eigenvalues	1.54	1.28	1.13
Variation explained	26%	21%	19%
Barn Swallow			
Mixed	0.599	0.256	−0.216
Crop	0.183	**0.704**	0.512
Coprophilous	0.030	**0.887**	−0.189
Oil-seed rape	0.030	−0.052	**0.904**
Other pests	**0.756**	0.018	0.039
Non-crop	**0.749**	−0.013	0.248
Eigenvalues	1.53	1.35	1.22
Variation explained	25%	23%	20%
House Martin			
Mixed	0.013	**0.769**	0.248
Crop	**0.715**	−0.061	−0.247
Coprophilous	−0.074	0.022	**0.870**
Oil-seed rape	−0.073	**0.766**	−0.240
Other pests	0.684	0.495	−0.046
Non-crop	**0.717**	−0.242	0.407
Eigenvalues	1.50	1.49	1.10
Variation explained	25%	25%	18%

elements — Ca, Zn, Cu, Co — and three non-essential toxic ones — As, Pb and Cd (Table 2). Interestingly, we observed that the faecal concentrations of Ca and Zn were markedly higher in Barn Swallows than in Common Swifts (1.7 and 4.9 times for these two elements respectively) and House Martins (1.4 and 28.1 times respectively). The faecal concentration of Cu was highest in House Martins, and its average concentration was 1.8 and 3.2 times lower in Common Swifts and Barn Swallows respectively. The Co level seemed to differ over a relatively small range among the three species, but because of the large consistency of concentrations in individual faecal sacs (confirmed by the very low standard errors) its content was significantly lower in Common Swifts than in the other two species. In contrast, the As concentration was highest in Common Swifts, being 1.3 and 1.6 times higher than in Barn Swallows and House Martins. The faecal concentrations of Pb and Cd showed similar gradients: the highest in House Martins, intermediate in Barn Swallows, and the lowest in Common Swifts. The faecal concentrations of Pb and Cd varied significantly among all three species (Table 2).

As in the case of dietary composition (see Supplementary data S4), we observed significant differences in the faecal concentrations of elements between 2011 and 2012 for Common Swifts with respect to Na, Ca, Mn and As (ANOVA, df = 1 and 55, $p \leq 0.021$), Barn Swallows with respect to Na, Mg, Fe, Cu, Mn, As, Pb and Cd (ANOVA, df = 1 and 64, $p \leq 0.0005$) and with respect to House Martins for Fe, Zn, Cu, Pb and Cd (ANOVA, df = 1 and 58, $p \leq 0.046$).

Our initial analysis of the relationship between the biomasses (mg d.w.) of the six functional prey groups and the concentrations of the 12 elements showed a distinctly variable number of statistically significant correlations across the various species (Supplementary data S3 and S4).

The results of the General Regression Model, applied to explain the faecal concentrations of the elements, showed different explanatory powers of the effects of dietary principal components and a variable number of statistically significant fits of final full models for the three species of aerial insectivores (Table 3). The highest number of significant models ($n = 7$) obtained for the Barn Swallow: Na (PC1: other pests + insects from non-crop habitats; the latter was a negative effect); Mg, Fe and Mn (PC1; for all these metals); As (PC1 and PC2: insects from crop habitats + coprophilous taxa; the latter was a negative effect); Pb and Cd (PC1 and PC2; the former was a negative effect). For the House Martin, the GRM yielded two significant fits: Cu (PC1: insects from crop + non-crop habitats, insects from mixed and non-crop habitats) and As (PC2: insects from mixed habitats + oil-seed rape pests). Lastly, there was only one significant fit for Common Swifts: Mn (PC2: insects from mixed and non-crop habitats). Summarising, the ranking of (statistically significant) full models in decreasing order of percentage of explained variance was the following; for Common Swifts — Mn (20%); for Barn Swallows — Cd (31%), Pb (29%), Na (23%), Mn (23%), As (22%), Mg (13%) and Fe (13%); and for House Martins — Cu (19%) and As (13%) (Table 3).

Lastly, Fig. 2 depicted the relationship between the percentage of biomass of oil-seed rape pests and pooled biomasses of other prey groups, and the concentration of two non-essential toxic metals, which significantly correlated with the dietary data both in the previous analysis of partial correlation (Supplementary data S4) and the multivariate GRM (Table 3).

Table 2
Comparison of the average (± SE) concentration (ppm d.w.) of 12 essential and non-essential elements determined in faecal sacs from nestlings of three sympatric aerial insectivorous feeding birds sampled in 2011 and 2012.

Element	All three species	Individual species[1]			Results GLM comparison between species[2]
		Common Swift	Barn Swallow	House Martin	
Na	839.07 (±178.32)	524.43 (±261.34) A	1179.76 (±379.52)	776.26 (±242.92) B	F = 2.54, p = 0.082
K	72.48 (±0.68)	70.50 (±0.78)	75.27 (±0.88) A	71.28 (±1.60) B	F = 2.88, p = 0.059
Ca	970.78 (±95.11)	728.40 (±131.72) A	1250.17 (±218.29) B	893.71 (±96.01) B	F = 13.06, p < 0.0001
Mg	76.16 (±4.33)	79.97 (±6.67)	82.02 (±8.30)	66.10 (±7.10)	F = 1.50, p = 0.226
Fe	55.79 (±15.28)	31.38 (±5.41)	32.86 (±7.42)	104.20 (±45.20)	F = 0.61, p = 0.545
Zn	11.64 (±9.03)	5.77 (±1.93) A	26.44 (±25.01) B	0.94 (±0.12) C	F = 13.58, p < 0.0001
Cu	1.01 (±0.33)	0.90 (±0.10) A	0.51 (±0.06) B	1.65 (±1.00)	F = 3.90, p = 0.022
Mn	0.33 (±0.02)	0.34 (±0.02)	0.25 (±0.01) A	0.42 (±0.04) B	F = 2.52, p = 0.083
Co	1.07 (±0.01)	1.06 (±0.01) A	1.08 (±0.01) B	1.08 (±0.01) B	F = 9.53, p = 0.0002
As	0.23 (±0.01)	0.29 (±0.02) A	0.23 (±0.01) B	0.18 (±0.01) C	F = 21.61, p < 0.0001
Pb	0.95 (±0.05)	0.47 (±0.03) A	0.91 (±0.02) B	1.44 (±0.11) C	F = 71.15, p < 0.0001
Cd	11.15 (±0.19)	8.40 (±0.36) A	11.71 (±0.09) B	13.15 (±0.10) C	F = 89.26, p < 0.0001

[1] Samples sharing a letter or without any letter are not significantly different in the *post-hoc* comparison.
[2] In all cases df = 2 and 180.

Table 3
All effects (β-values) of dietary principal components (PC1–PC3) of the biomasses (mg d.w.) of six functional prey groups from General Regression Models explaining the concentrations of 12 essential and non-essential elements in individual faecal sacs from nestlings of three sympatric avian aerial insectivores; the principal components for individual species represent various prey groups (see Table 1 for details): mixed (mix), crop (crp), coprophilous (cop), oil-seed rape (oil), other pests (oth) and non-crop habitats (non); the asterisks denote the significance level for individual principal components: * — p < 0.05, ** — p < 0.01, *** — p < 0.001.

Element	Common Swift						Barn Swallow						House Martin					
	PC1 (crp + cop)	PC2 (mix + non)	PC3 (oil)	Final model			PC1 (oth + non)	PC2 (crp + cop)	PC3 (oil)	Final model			PC1 (crp + non)	PC2 (mix + oil)	PC3 (cop)	Final model		
				R^2	$F_{3,53}$	p				R^2	$F_{3,62}$	p				R^2	$F_{3,56}$	p
Na	0.17	0.22	−0.05	0.08	1.55	0.213	0.39***	−0.21	−0.19	0.23	6.22	0.001	0.20	−0.05	−0.01	0.04	0.80	0.497
K	−0.22	0.04	−0.16	0.07	1.37	0.263	0.20	−0.16	−0.05	0.07	1.57	0.206	−0.01	0.04	0.02	0.01	0.04	0.989
Ca	−0.12	−0.11	−0.04	0.03	0.50	0.683	−0.02	−0.01	−0.11	0.01	0.26	0.851	0.20	−0.17	−0.16	0.10	1.98	0.128
Mg	0.16	0.10	−0.19	0.07	1.31	0.280	0.35***	−0.05	−0.07	0.13	2.97	0.038	0.32*	−0.01	0.02	0.11	2.21	0.097
Fe	0.23	−0.11	−0.16	0.09	1.75	0.167	0.27*	−0.07	−0.23	0.13	3.12	0.032	0.19	0.05	0.18	0.07	1.51	0.222
Zn	0.04	0.06	−0.27*	0.08	1.50	0.224	0.29*	0.02	−0.14	0.10	2.43	0.073	0.16	0.12	−0.03	0.04	0.85	0.475
Cu	0.15	0.05	−0.05	0.03	0.48	0.696	0.25*	−0.16	−0.14	0.10	2.42	0.075	0.40**	0.14	0.11	0.19	4.44	0.007
Mn	0.21	0.35**	−0.19	0.20	4.55	0.007	0.39***	−0.21	−0.19	0.23	6.22	0.001	0.20	−0.05	−0.11	0.04	0.82	0.488
Co	0.15	0.12	−0.30*	0.13	2.62	0.060	0.32**	0.02	0.10	0.11	2.60	0.060	0.09	0.01	0.02	0.01	0.16	0.921
As	−0.12	0.01	0.08	0.02	0.37	0.773	0.36**	−0.30*	−0.01	0.22	5.74	0.002	0.24	0.25*	−0.14	0.13	2.86	0.045
Pb	0.19	−0.10	0.01	0.05	0.86	0.469	−0.30**	0.45***	0.01	0.29	8.34	0.001	0.06	0.30*	0.14	0.12	2.45	0.073
Cd	−0.04	0.05	−0.04	0.01	0.10	0.960	−0.29**	0.47***	0.09	0.31	9.39	0.001	0.07	−0.16	−0.07	0.04	0.71	0.551

4. Discussion

Firstly and quite unexpectedly, our study showed that the faecal concentrations of seven (out of 12) elements (Ca, Zn, Cu, Co, As, Pb and Cd) varied markedly both among the three bird species and exhibited a wide variability across the different faecal samples from the individual species. As we had anticipated, most of these relations could be linked primarily to the variable dietary composition of the birds, expressed as six functional invertebrate prey groups representing different trophic/dietary guilds of insects. Therefore, Common Swifts, with the lowest faecal levels of Ca, K, Fe, C, Pb and Cd and the highest As concentration, primarily consumed prey representing low trophic, typical phytophagous/highly chitinised prey, such as small-bodied beetles (*Ceutorhynchus* spp. and *Meligethes* sp.), which are pests of oil-seed rape. Barn Swallows, representing an intermediate trophic position, while catching a variety of prey, consumed the highest biomass of coprophilous/saprophagous insects, which could explain the highest levels of minerals like Ca, K, Ca, Mg and Zn in their faeces. The trophic status of House Martins can be classified as the highest, since they consumed the largest number of predatory insects, such as spotted ladybirds *Coccinella* spp. (including the samples analysed in this study), which most likely explains the highest level of Fe, Cu, Mn, Pb and Cd in their faeces. We may therefore infer from the above that our results confirm the general rule of increasing levels of minerals and non-essential elements with the trophic position of a prey species (Hunter et al., 1987; Vermeulen et al., 2009; Schipper et al., 2012). In addition, the level of faecal elements could also be indicative of the close insect-soil/decomposed substrate link (Barn Swallows) or even the application of agrochemicals (As) (Common Swifts).

Secondly, the dietary contribution of the biomass of functional invertebrate prey groups representing mainly insects characteristic of agricultural areas in the temperate regions of Europe was significantly correlated with the concentrations of all the elements in both univariate partial correlation and multivariate (GRM) analysis; the intensity of these interactions varied between the target species and the elements, however. The most conspicuous effects of diet (in both analyses) were obtained for the Barn Swallow, being the species with the relatively greatest dietary variation and a greater proportion of coprophilous/saprophagous taxa in the biomass consumed, displayed the greatest number of significant diet–faecal element relationships and most fitted GRM models. In particular, this confirms our prediction that the biomass of consumed coprophilous (including saprophagous) taxa and insects living in crop habitats (loaded as PC2) was positively correlated with the faecal concentrations of toxic elements, which most likely originate from the type of substrate (soil, manure) consumed by these insects (Hunter et al., 1987; Gräff et al., 1997). Overall, these findings may suggest that the food consumed by Barn Swallows contains relatively more essential elements, the surplus of which (i.e. the non-assimilated amount) is probably eliminated through the faeces. Importantly, both our univariate (partial correlation) and multivariate (GRM) analyses revealed the highest number of significant relationships/effects for the toxic metals (As, Pb and Cd), including the highest percentage of variance explained in the full models (up to 31% for the Cd concentration in Barn Swallow faeces), which generally may reflect the intensive excretion of these non-essential element through the faeces.

Faecal samples, primarily of Common Swifts, with a higher percentage biomass of oil-seed rape insect pests, showed significantly higher levels of As, most likely derived from the insecticides applied for the chemical control of insect pests on these crops. It seems that the lack of significant relationships for the vast majority of the elements (except for Mn, but see the comment below) for Common Swifts could be due to the similar diet and high percentage of oil-seed rape insect pests in their diet. Furthermore, it is obvious that the elemental content in the body of this same insect species could vary substantially depending on the concentration of a given element in the food/substrate (Gräff et al., 1997;

Eeva et al., 2005; Ding et al., 2013; Green and Walmsley, 2013; Ardestani et al., 2014). In practice this could mean that some species or even groups of prey, occurring in the faeces of the target bird species, such as oil-seed rape pests or other insect species, exhibit large differences in levels of elements, for instance, associated with the application of agrochemicals. This could be an additional explanation for the observed significant intraspecific differences in concentrations of some elements between the two years of the study.

On the other hand, some of the relationships that we obtained in our study are not entirely clear. This is partly due to the fact that our functional prey group approach is a formal generalisation of dietary composition, as a result of which some prey taxa, like predatory (= higher trophic) insects, e.g. spotted ladybirds *Coccinella* spp. or some carabid beetles, were classified in a more synthetic guild. In House Martins only the concentration of Pb was significantly correlated with the biomass of insects from mixed habitats (which contained ladybirds). Similarly, GRM showed that insects from mixed habitats and oil-seed rape insect pests (loaded as PC2) positively affected the Pb level. It seems, therefore, that further detailed analyses taking the trophic levels of prey taxa in our sample into account may throw some light on this problem.

Other potential explanations for the observed interspecific differences in the faecal concentrations of elements resulting from factors related to the individual bird species are also possible. For instance, the flight and hunting height of these three species is different, being lower for the Barn Swallow, medium for the House Martin and higher for the Common Swift (Waugh, 1978). Both Barn Swallow and House Martin use mud to build their nests and/or even during bad weather they can pick prey from the ground (Turner, 2006), so dust/soil ingestion could be a significant way of exposure in these two species feeding closer to the ground surface. Moreover, it should be stressed that although the three species of aerial insectivores are defined in our study as sympatric, the foraging range of Common Swift is most likely much larger than in the both hirundine species (Lack and Owen, 1955; Waugh, 1978; Turner, 2006). Some differences in the ability to excrete variable amounts of elements resulting from different physiological features of species in the context of their phylogenetic differences (as between swifts and hirundines) are also possible.

An important question, already mentioned in the Introduction, was to relate dietary composition to the faecal content of minerals. In comparison with previously published results on the content of elements in avian faeces or guano, including studies of non-essential elements conducted in both unpolluted and polluted areas, we observed surprisingly low levels of both essential and non-essential elements, and only the Cd level seems to be high and indicative of environmental exposure (reviewed in Kamiński and Wołosiuk, 1995). For instance, the Ca concentrations in the faeces of Pied Flycatcher nestlings, with a more differentiated diet also containing flying insects, were 5337 ppm and 2751 ppm in polluted and unpolluted sites respectively (Eeva et al., 2005). With regard to only the latter, lower value, Ca concentrations in our sample were 3.8 times (Common Swift), 2.2 times (Barn Swallow) and 3.1 times (House Martin) lower (cf. Table 2). The potential explanation of these apparent differences seems to be that these aerial insectivores took exclusively highly chitinised insects, and that soft-bodied prey types with a high Ca content like larvae, moths or spiders were lacking in their diets (Finke, 2007, 2008; Eeva et al., 2005). Since we have no data on the elemental content in prey taken by the three target bird species and there is no data in the literature on some essential elements determined in the excreta of insectivorous birds, it seems that for a detailed comparison one could use published data on the nutrient composition of insects. We believe that such a comparison might shed light on the level of assimilation/excretion of some elements resulting from the digestion of food and the production of faeces in growing nestlings of insectivorous birds in the context of their physiological demands for nutrients, because the excretion patterns of animals provide useful information on the probable mechanisms of metal

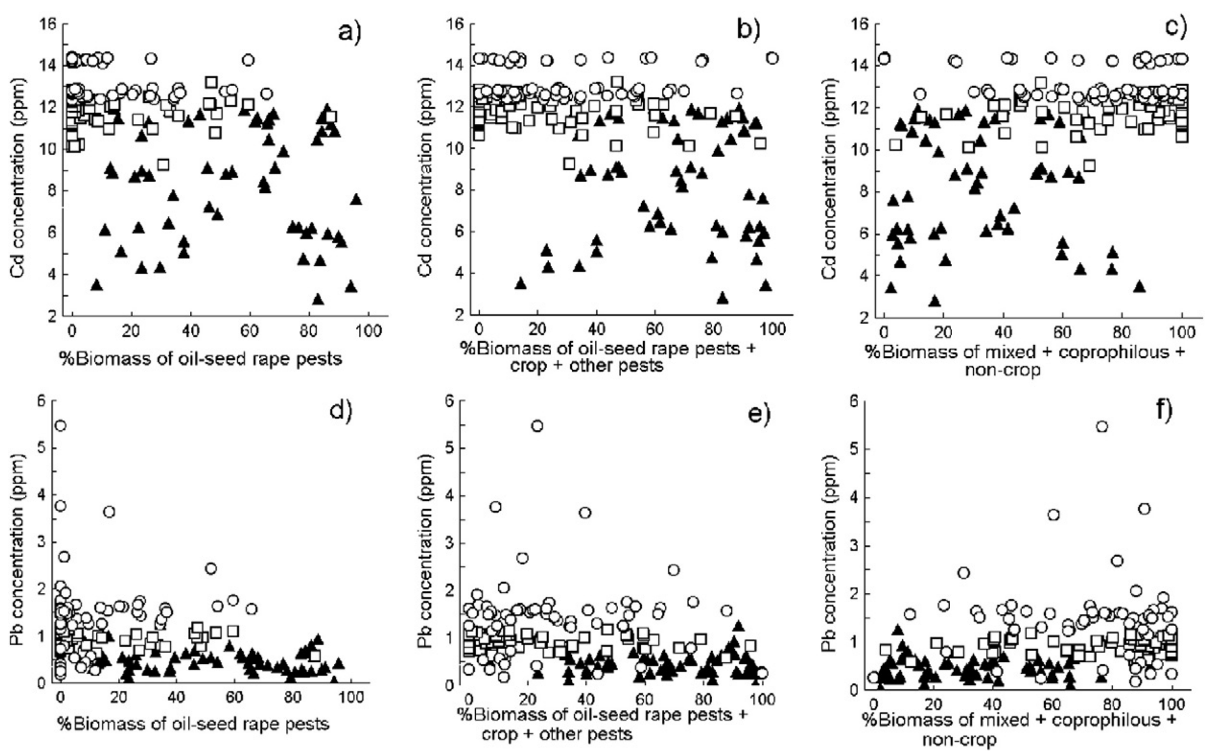

Fig. 2. Relationships between the percentage biomass of oil-seed rape pests, biomass of crop-provisioned invertebrates (pooled oil-seed rape pests, crop and other pests) and pooled biomass of other invertebrates (mixed, coprophilous and non-crop habitats) and concentrations of cadmium (a–c) and lead (d–f) in individual faecal sacs of three sympatric aerial insectivores, Common Swift (▲), Barn Swallow (□) and House Martin (○).

detoxification (Kozlova et al., 2000). In practice, one can assume that the markedly lower levels of elements in our sample than in the bodies of insects (the minimal values reported in the literature are given below) are probably indicative of the intensive assimilation of a given element. The opposite relationship, i.e. a considerably higher level in our sample, might translate into its potential excretion through the faeces. For this comparison we used data on the nutrient composition of a number of invertebrates compiled by Finke (2008), which can provide a baseline nutrient concentration for many insect species. The average mineral content reported for the whole body of a dozen species of Coleoptera, Lepidoptera larvae, Orthoptera, Isoptera, Hymenoptera and Diptera was: Ca — 2837 ppm (range = 400–24,800), Mg — 2100 ppm (280–11,500 ppm), K — 10,718 ppm (1170–32,580 ppm), Na — 4865 ppm (300–33,380 ppm), Fe — 275 ppm (21–1448 ppm), Zn — 165 ppm (61–297 ppm), Cu — 23.2 (2–137 ppm) and Mn — 110.5 ppm (3–660 ppm) (calculated from Finke, 2008). Comparing these data, our findings showed particularly low levels of five elements: K (approximately 16 times lower in our sample than the minimal value reported in Finke, 2008), Mg (c. 4 times lower), Zn (c. 2–65 times lower, depending on the species), Cu (up to c. 4 times lower) and Mn (up to c. 12 times lower) (cf. Table 2; Finke, 2008). The faecal levels of three other nutrients (Na, Ca, Fe) obtained in our study were relatively low, although they concur with previously reported concentrations of these elements in insect bodies (cf. Table 2; Finke, 2008). Obviously, however, all these relations constituted only a specific proxy of the unknown content of elements in the food consumed. Furthermore, it should be acknowledged that the chitin of most insects contains only insignificant amounts of minerals, although some pupae or larvae of flies contain significant amounts of Ca in their cuticle (Finke, 2007). On the other hand, it should be remembered that in our chemical analyses we used whole faecal sacs, which contained both the remains of the chitinous exoskeletons of insects and highly digested food remains. Therefore, given that chitin is rather a poor transmitter of some elements, including non-essential elements, one might speculate that a large proportion of elements in faeces does not come from the remains of the chitinous exoskeletons, but from the highly digested food remains, which are probably also remains of soft tissues or gastrointestinal tract contents (= food) of insects. However, this interesting question with clear potential implications for the biotransfer of elements deserves further detailed study.

5. Conclusions and research implications

Our findings have clearly demonstrated that the contribution of avian predator species with a similar trophic position to the biotransfer of elements (tracked in their faeces) is a complex phenomenon, and determining solely the elemental content without describing the dietary composition in a faecal sample is insufficient to assess the spatio-temporal variability of elements in avian excreta. In practice, this implies certain limitations to the application of faeces in the biomonitoring of trace metals, especially with respect to species of predators characterised by a highly variable diet, such as aerial vertebrate insectivores. To a lesser degree, this limitation probably relates to species with a similar (mono)diet, like some marine birds or predatory vertebrate species that consume a relatively uniform composition of prey, as piscivorous/plankton-eating birds or mammals (Yin et al., 2008; Signa et al., 2013). On the other hand it should be acknowledged that the same prey type can vary enormously in levels of body elements, which is largely dependent on the concentrations of elements in the ingested food (e.g. Gräff et al., 1997; Finke, 2007, 2008; Green and Walmsley, 2013). In our case, therefore, this limitation concerns primarily insects living in crop habitats, where agrochemicals are applied with varying intensity, which may directly translate into the spatio-temporal differentiation of the bioaccumulation levels of some elements.

On the other hand, we realise that our study has a correlative character, and because of the multivariate nature of the dietary data obtained from the faecal sacs examined (including the diverse grouping of functional prey groups in PCA), the partitioning of effects of dietary composition on the faecal element content could in some cases be ambiguous. Nevertheless, the majority of the results are biologically interpretable in the context of previous findings on the biotransfer of elements from lower to higher trophic levels of the food chain. Hence they may make an important contribution to knowledge about the biotransfer of elements in an aerial food web, including the little known process of the flow of some minerals from insect food via aerial insectivorous predators to faecal deposits, and have some clear practical implications for further ecotoxicological studies.

Overall, our findings suggest that the low faecal levels of the majority of essential elements are a result of their intensive assimilation in the gastrointestinal tract of nestlings. Moreover, in the light of previous studies, which demonstrated the excretory mechanism of non-essential elements through faeces (Świergosz et al., 1998; Eeva et al., 2005; Berglund et al., 2010), our findings appear to confirm this pathway of elimination for As, Pb and Cd. Nonetheless, only the level of Cd was high, which may signify greater environmental exposure to this toxic element in our study area. The high content of Cd recorded in the faeces of the target bird species confirms our previous studies, which showed an elevated level of this toxic element in various invertebrates and tissues of birds from farming areas of Poland (Kamiński and Wołosiuk, 1995; Orłowski et al., 2012, 2014b). This is most likely a result of the relatively high Cd content in the soil, the average value of which for the whole country is 0.69 to 0.78 ppm Cd; in our study area levels of up to 0.23 ppm Cd were reported (Terelak et al., 2008).

Importantly, the Cd concentration varies among the three target species. Despite the relatively lowest concentration observed in Common Swifts (8.40 ppm Cd), these values indicate environmental exposure to this non-essential element. As we demonstrated above, the Cd levels in the faeces of the three target species most likely reflect the trophic levels of their prey: low (primarily phytophagous prey; Common Swifts) > intermediate (highly variable diet; Barn Swallows) > high (predatory insects are preyed on; House Martins). In this scenario, it is particularly interesting to identify the biotransfer of Cd in Common Swifts, which consumed primarily two species of oil-seed rape insect pests. Owing to their ability to hyperaccumulate Cd, oil-seed rape crops are known to be an important means for the phytoremediation of Cd-polluted soil (reviewed in Varkey et al., 2013). However, the highest Cd levels recorded in oil-seed rape plants growing in soil highly contaminated by this element (up to 22.5 ppm Cd) did not exceed 2.66 ppm Cd (Ciecko et al., 2001). Since this value is 3.3 times lower than the Cd level in faeces of Common Swifts, it should be assumed that biomagnification of Cd occurs along the food chain described in our study (oil-seed rape plant–insect pests of rape–aerial insectivores). On the other hand, significantly higher Cd and Pb concentrations in the faeces of Barn Swallows and House Martins than in Common Swifts, suggest that the biomagnification of both these elements (apart from phytophagous insects) increases gradually, embracing insects from higher trophic levels. These findings imply that in our study system the cross-boundary transfer of contaminants by aerially foraging birds through their faeces concerns primarily Cd. However, taking into account the results of previously published studies showing high faecal concentrations of other non-essential elements (Pb, As) or residues of pesticides, the large accumulation of faeces of birds has potential consequences for the local biogeochemical cycle and quality of environment. We advocate the need for further ecotoxicological studies aimed at evaluating spatial variation in the biomagnification of non-essential elements and other agricultural-derived contaminants along the food chain of biota in farmed areas along a gradient of agricultural production intensity.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2015.02.078.

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