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Variability in nestling diet of European hoopoes: annual and sampling effect

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Abstract. The aim of the study is to get a representative picture of the diet composition of hoopoes in vineyards as specific man made habitats in Central Europe. Therefore diet composition and its interannual variability and the representativeness of two sampling techniques have been studied in hoopoe nestlings, *Upupa epops* during two breeding periods. Altogether, 1081 prey items were identified and classified into ca. 90 species, 32 families and 11 orders of invertebrates. Regarding interannual variation, the number of prey items per nestbox did not differ between years in the same nestboxes. A within-nest comparison between the two sampling methods revealed a significant difference in the number of prey items for four categories, namely orthopterans, "other beetles", arachnids and lepidopterans. Comparing the two sampling methods, revealed reversed results regarding the proportion of the main prey categories; e.g. scarabaeid larvae, abundant in the camera samples, were less frequent in faeces, whereas "other beetles" were common in faeces, but were only occasionally detected in the camera recordings. The occurrence of the earthworms in the hoopoe's food is novel. We finally discuss advantages as well as the drawbacks of both methods and the possibility to use both these contrasting, but non-invasive techniques.

Key words: food, foraging ecology, hoopoe, methods, seasons

Introduction

A detailed knowledge of the diet composition of a species is an important parameter in avian ecology. Insectivorous birds are often opportunistic and polyphagous and there are a number of factors influencing individual diet variability (Rosenberg & Cooper 1990). Offspring survival often depends on the availability of large insects (Purger 1998, Fournier & Arlettaz 2001, Pedersen et al. 2012), insect population dynamics (Hoi et al. 2004, Arlettaz et al. 2010, García-Navas & Sanz 2011) and weather conditions (Dawson & Bortolotti 2000, Radford & Du Plessis 2003), e.g. low ambient temperatures or rainy periods affect insect activity and consequently prey availability for offspring (Morrison & Bolger 2002, Arlettaz et al. 2010). Thus, weather conditions may be in particular important to explain variation in the diet composition between years.

To study bird diet, a variety of methods including ligatures (e.g. Johnson et al. 1980), emetics (e.g. Carlisle & Holberton 2006), gut (e.g. Harris & Wanless 1993) or faecal analyses (e.g. Moreby & Stoate 2000, Cummins & O'Halloran 2002) and visual observations including camera recordings (e.g. Fournier & Arlettaz 2001) have been proposed. While some methods, e.g. invasive ones, are not viable for threatened species (Ralph et al. 1985, Rosenberg & Cooper 1990, Parrish et al. 1994, Hanula & Franzreb 1995), others may produce unrepresentative results of dietary composition. For example, camera recordings are suitable to recognize larger or common prey items, but inconspicuous food items could be overlooked (Rosenberg & Cooper 1990). On the other hand, faecal analyses could widen information on smaller prey and are characterized by easy sampling without harming the birds (Michalski et al. 2011, Veľký et al. 2011).

Regarding sample method, it is also important to consider the sampling period in relation to prey availability (Mizutani & Hijii 2002, Visser et al. 2006,

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Goławski 2007). In particular for faecal analysis, it is important to indicate whether droppings are obtained fresh, means directly from nestlings of known age (e.g. Brickle & Harper 1999, Moreby & Stoate 2000, Cummins & O'Halloran 2002) or dry, with no further information about nestling age (e.g. Dit Durell & Kelly 1990). Nestling age could be important in relation to the diet composition especially, when the diet and food availability change during the nestlings feeding period (e.g. Brickle & Harper 1999, Mitrus et al. 2010). Several studies have used more than one sampling method in order to increase the representativeness of the diet composition of a given species (e.g. Tryjanowski et al. 2003, Selås et al. 2007, Šotnár et al. 2008, Pagani-Núñez et al. 2011). Faecal analysis for example has been used in combination with photography and gut analysis (e.g. Kleintjes & Dahlsten 1992), with visual observation (e.g. Scheiffarth 2001), with neck-collars (e.g. Dyrcz & Flinks 2003) and with pellets analysis (e.g. Sánchez et al. 2005). A few studies have also used different methods in order to identify within nest and within year variation in the diet composition (e.g. Hirschfeld & Hirschfeld 1973, Poulsen & Aebischer 1995, Moreby & Stoate 2000, Dyrcz & Flinks 2003). Only a few studies describe the food variability of bird species in man made habitats as vineyards.

Vineyards are specific habitats regarding habitat structure (e.g. provide large portions of bare ground), composition, phenology and occurrence of the main arthropod prey available for ground-probing birds where the knowledge on their feeding habits are particularly scarce (Arlettaz et al. 2012). Insectivorous birds as hoopoes (see in Schaub et al. 2010) have been considered to essentially contribute to control insect pests in vineyards. The European hoopoe, *Upupa epops* is specific regarding its foraging technique and bill morphology (Barbaro et al. 2008, Arlettaz et al. 2010, Tagmann-Ioset et al. 2012). Besides that it is considered as one of the most endangered bird species in western and central Europe (BirdLife International 2004).

In the current study, we examined the diet composition and food of hoopoe parents delivered to their nestlings, in a vineyard habitat of Lower Austria (for details see methods section). To achieve representative results we used two sampling methods, namely camera recordings and faecal analyses. Additionally, we compared the variation of nestling diet composition between the two sampling methods and successive years. With regard to insectivorous birds, there is surprisingly few information about interannual variability in diet composition in a repeatable manner (see Bańbura et al. 1994). Therefore to compare diet composition between the two years we used the same nestbox in the same breeding habitat and the same sampling method. Due to the varying weather conditions we predict between-year differences in food availability and examined whether they are reflected in the diet composition. To compare variation in prey composition between the two sampling techniques (camera recording and faecal sampling) we used the same nests but within the same year. Hoopoes represent a suitable model species for using in particular camera recordings, because they are single prey loaders (Orians & Pearson 1979) – parents usually bring only one large prey item per feeding visit (e.g. the cockchafer larva *Melolontha melolontha*). For this reason most previous hoopoe studies conducted sampling via direct visual observations or camera recordings (Krištín 1993, Fournier & Arlettaz 2001, Stange & Havelka 2003, Pühringer 2008, Arlettaz et al. 2010, Rieder & Schulze 2010). While camera recordings allow us to recognize larger (> 20 mm) and soft-bodied prey items (larvae), faecal analysis may reveal information about small prey items that survive digestion and are diagnostic. Therefore, we predict that the camera and faeces sampling methods might mirror diverging diet compositions. In summary, the following three aims have been formulated for the present study, namely to determine the i) diet composition of hoopoe nestlings in vineyard habitats based on camera recordings and faecal sampling; ii) interannual variation in the diet composition in a repeatable design (using the same nestboxes in successive years and based on camera recordings only) and iii) differences in diet composition obtained by the two sampling techniques.

Material and Methods

Study species and study area

Hoopoes belong to ground-foraging insectivorous birds, preferring mainly soft and bigger food items (e.g. caterpillars, cockchafer larvae; Fournier & Arlettaz 2001, Krištín 2001). European hoopoes are long-distance migrants, wintering in Africa (Bächler et al. 2010). In Central Europe, males usually settled in their territories by mid April, and leave in August. They inhabit open areas with bare or sparse vegetated ground that represents a suitable foraging habitat to search for ground-dwelling larvae and insects (Schaub et al. 2010). Hoopoes belong to the group of cavity-nesting birds, breeding mainly in trees cavities, abandoned burrows in cliffs or walls, as well

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as nestboxes (Glutz von Blotzheim & Bauer 1994, Krištín 2001).

The study was conducted at the Wagram area in Lower Austria (119 km^2, 230-350 m a.s.l., 48.45°-48.47° N, 15.66°-15.73° E). The hoopoe population breeds there exclusively in wooden nestboxes (50 cm long, 30 cm wide and 30 cm high) that were covered inside with bark dust. They usually breed twice a year and the most of the pairs started egg laying in May. After fledging of young, the second breeding attempt usually started in June. In extreme cases, some pairs are engaged in offspring care until early August, but all these late attempts have been unsuccessful.

The study area represents a traditionally cultivated landscape consisting of south-exposed slopes, covered mostly by vineyards (80 %), with the remaining 20 % consisting of orchards with small trees, patches of woodland habitat, steppe grasslands and sandy cliffs ("loess"). The vineyard habitat consists mostly of bare soil that is regularly or irregularly ploughed, what ensured a mellowness of the soil. Such bare grounds, unploughed areas around the wine trunks, short grassland and their ecotones are most preferred by hoopoes as a foraging microhabitat because it seems rich in ground-dwelling larvae (Romanowski & Żmihorski 2008, Hoste-Danylow et al. 2010). We did not establish specific criteria in order to assess e.g. foraging microhabitat or placement of nestboxes. Habitat composition was not assessed, but all habitats surrounding the studied nestboxes were similar (with proportion of bare ground and grassland 85:15 %). Due to the provision of 300 nestboxes, the population increased from two breeding pairs in the whole study area in 2004 (2 pairs/100 km^2) to 60 pairs/100 km^2 in 2010. For this study in total, 40 nestboxes were used for general information on hoopoe diet composition (Fig. 1, Table 1).

Camera recordings and faeces sampling

During the breeding period in 2009 and 2010, the general information on the nestling diet was gathered by camera recordings, when the nestlings were between 8 and 27 days old. The recordings were gathered from May 24 to August 5. Data were obtained from a total of 38 broods (13 nests in 2009, 25 nests in 2010, 27 nestboxes in total). Each nestbox was recorded for 120 min once per season. The recording devices were installed 0.5-1 m from the entrance hole. In order to minimize disturbance, all equipment was well hidden. Recordings were made in the morning (6:00-9:00 a.m.) or in the late afternoon (5:00-8:00 p.m.). All recordings were processed with the program "iMovie". Depending on image quality, we identified each food item to the highest possible taxonomic

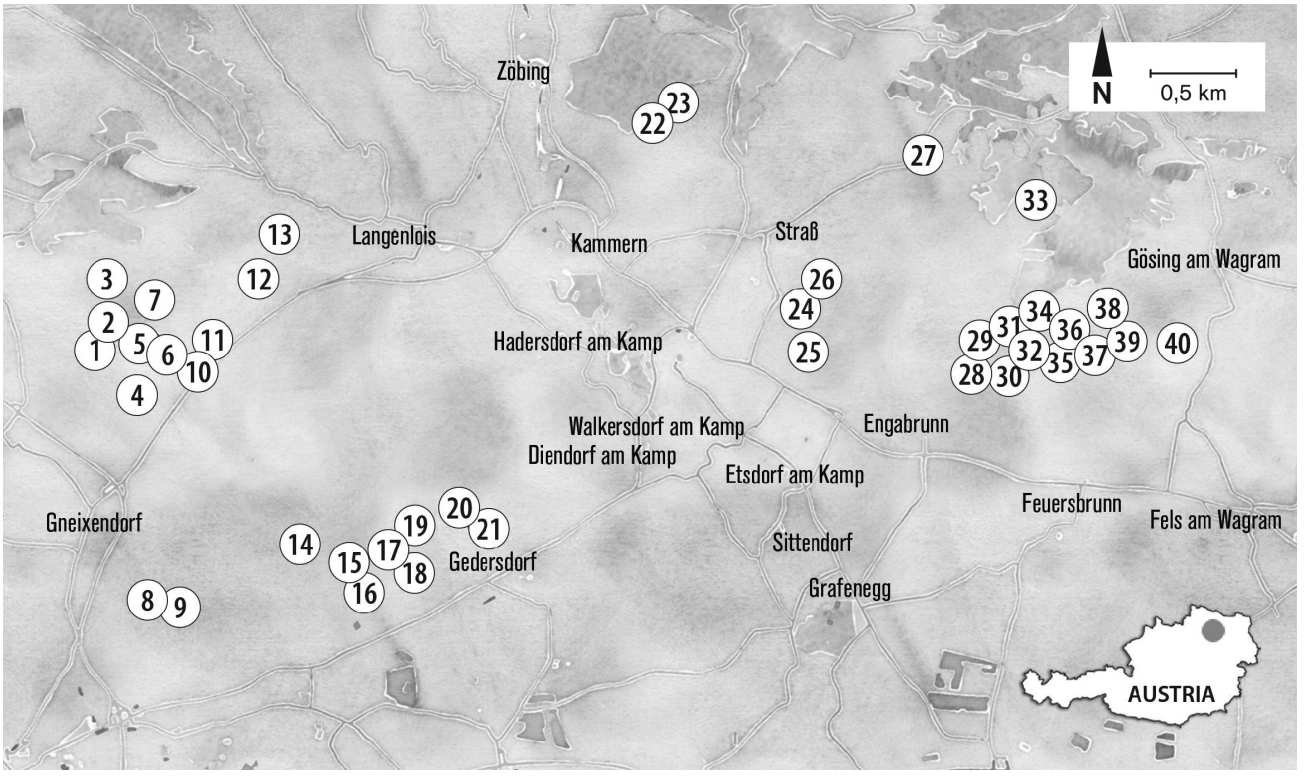


Fig. 1. Location of 40 studied hoopoe nestboxes in the Wagram area, Lower Austria.

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Table 1. The abundance and dominance (n, n%) of prey taxa in hoopoe nestling diet obtained by two methods in 2009 and 2010.

	Camera recordings 2009		Camera recordings 2010		Fecal analysis 2010	
Taxon	n	n%	n	n%	n	n%
Arachnida						
Opilliones					1	0.2
Araneae g. sp.	1	0.4	12	2.6	27	5.7
Lycosidae					1	0.2
Thomisidae			1	0.2		
Scarabaeoidea larvae	226	81.6	220	47.4	95	20.1
Other Coleoptera						
Coleoptera imagos g. sp.	2	0.7	3	0.6	9	1.9
Coleoptera larvae g. sp.			7	1.5	1	0.2
Carabidae g. sp.			1	0.2	27	5.7
Carabus sp.					36	7.6
Pterostichus sp.			8	1.7	5	1.1
Curculionidae					1	0.2
Tenebrionidae					1	0.2
Byrrhus sp.					1	0.2
Elateridae larvae			7	1.5	8	1.7
Scarabaeoidea imagos g. sp.					6	1.3
Aphodidae					3	0.6
Cetonia aurata			2	0.4	6	1.3
Protaetia cuprea					1	0.2
Tropinota hirta					1	0.2
Valgus hemipterus					1	0.2
Geotrupes sp.	1	0.4			10	2.1
Amphimallon solstitiale			18	3.9	8	1.7
Anomala dubia					9	1.9
Copris lunaris					1	0.2
Onthophagus sp.					44	9.3
Silphidae g. sp.					5	1.1
Silpha sp.					12	2.5
Lepidoptera						
Lepidoptera larvae g. sp.	1	0.4	5	1.1	16	3.4
Lepidoptera pupae g. sp.					3	0.6
Lepidoptera imagos g. sp.					36	7.6
Saturniidae larvae			3	0.6	1	0.2
Noctuidae imagos	3	1.1			1	0.2
Noctuidae larvae	1	0.4	9	1.9		
Notodontidae larvae			3	0.6		
Nymphalidae larvae	1	0.4	10	2.2		
Orthoptera						
Acrididae g. sp.	3	1.1	5	1.1	23	4.9
Oedipoda caerulescens			8	1.7		
Gryllus campestris	3	1.1	7	1.5	30	6.3
Tettigonidae g. sp.					2	0.4
Decticus verrucivorus	1	0.4				
Tettigonia sp.					3	0.6

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Tettigonia viridissima	1	0.4	2	0.4	5	1.1
Other taxa						
Forficula auricularia			12	2.6	6	1.3
Diptera imagos g. sp.			6	1.3	2	0.4
Diptera larvae g. sp.	3	1.1				
Diptera pupae					1	0.2
Brachycera g. sp.			2	0.4		
Tabanidae imagos			2	0.4		
Tipulidae larvae			2	0.4		
Heteroptera g. sp.					2	0.4
Pentatomidae					5	1.1
Apidae			2	0.4		
Formicidae g. sp.			2	0.4		
Camponotus sp.					5	1.1
Vespidae					1	0.2
Myrmeleontidae					11	2.3
Lumbricidae g. sp.	1	0.4	1	0.2	-	-
No. of prey items identified	248	89.5	360	77.6	473	100.0
No. of unident. prey items	29	10.5	104	22.4	-	-
Prey items total	277	100.0	464	100.0	473	100.0

Explanations: n, abundance of taxa identified by both methods; n%, dominance of taxa identified by both methods; g. sp., abbreviation by prey taxon, as specimen was impossible to identify more precisely; the group Coleoptera larvae does not include the group Scarabaeoidea larvae; the genus *Geotrupes* includes also related genera; genus *Onthophagus* includes also genus *Euonthophagus*; bold taxa mark the main food groups in the study.

level. We also registered the date, the number of prey items per feeding and the developmental stages of prey items (larva, pupa or imago).

The faecal samples we obtained from 28 nests only in 2010. Samples were collected when the nestlings were 20-25 days old. It would have been optimal to obtain droppings directly from nestlings, but we avoided any unnecessary harm to nest and to have a negative influence on the breeding success. We found large faecal accumulations under the entrance holes of the nestboxes, because females usually removed droppings by just throwing them out of the hole. We collected approximately 3 cm^3 from the top of each faecal accumulation, which are probably most recent droppings. In this way, the sample was representative for the current age of the young in the nest. Faeces were preserved in 70 % alcohol and later dissected using a microscope with 6-50× magnification. Each sample was processed on a Petri dish by separating paired and unpaired prey body parts (e.g. wings, mandibles, legs, heads, etc.) to make an estimation of the numbers of individuals for each sample (Rosenberg & Cooper 1990, Kleintjes & Dahlsten 1992, Pechacek & Krištín 2004). Only sure identified larvae were categorized in particular prey taxa and all the unidentified larvae were added to the group "unidentified prey". We identified food remnants to the lowest possible taxonomic level using a comparative collection of arthropods (cf. Pechacek & Krištín 2004, Table 1). In multiple fragments of the same specimen, we counted only one unpaired fragment (head) or one mandible (left or right) or three pairs of legs, considering the relative size of specimen. In faecal samples, as well as in camera recordings, prey items were identified and prey size was determined according to Chinery (1987) and Giljarov (1964) to particular invertebrate groups.

Data analyses

Diet composition of hoopoe nestlings from all the nestboxes was characterized by the dominance (n%) of all identified food taxa collected in camera recordings (2009 and 2010) and in faecal samples (2010). In order to exclude the effect of different territories/habitats and nestling ages on the diet composition, the interannual variation in diet composition was tested using data from only 11 nestboxes where camera recordings were available from both years (2009 and 2010) (Fig. 1: boxes no. 11, 12, 14, 16, 20, 23, 26, 31, 32, 36 and 39).

In 2010, the comparison of the both sampling techniques was made in the same 10 nestboxes where

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camera recordings and faeces sampling were done and with approximately the same nestling age (Fig. 1: boxes no. 1, 9, 14, 15, 18, 19, 20, 27, 36 and 40). For the both comparisons, paired sample t-tests or Wilcoxon's signed-ranks tests were accomplished depending on whether results met normality (tested via a Kolmogorov-Smirnov test of normality).

To control for the effect of different nestling age, a paired t-test was applied to test differences in the age of broods in 11 nestboxes, where they were recorded in 2009 and 2010 as well as to test differences in 10 nestboxes, where both methods were used in 2010. The differences in the date of recordings of the same nestboxes in 2009 and 2010 were tested by paired t-test, too. Data of recordings were first converted to serial numbers of days in a year. The age of the nestlings in the 11 compared nestboxes did not differ between 2009 (average age was 19.5 days) and 2010 (average age was 17.1 days) (paired t-test $t = 1.732$, $p = 0.114$). Similarly, the date of recordings did not differ between both years (average day was 193rd day, i.e. July 12 in 2009 and 183rd day, i.e. July 2 in 2010) ($t = 1.692$, $p = 0.121$). Thus, we can assume that the variation in the diet composition between the two years is affected neither by differences in nestling age nor in differences in date of recording. There was also no nestling age difference in the 10 nests where food was analyzed by both methods (average age of recorded broods was 21.7 days and those which faeces were analyzed was 22.5 days) (paired t-test: $t = 1.546$, $p = 0.156$).

Difference between average size of prey items in camera recordings and faecal samples were tested using a Mann-Whitney U-test based on data from only 10 nestboxes mentioned above. The diversity of prey taxa was calculated by the Shannon-Wiener diversity index using natural logarithms. Diversities calculated from data obtained by both sampling methods in the same nestboxes were compared using Student's t-test (Poole 1974).

Data are presented as means ± standard error throughout. To take the possibility of very fragmented prey items (e.g. earthworms) into account, in faecal samples, the frequency of prey remnants was also calculated (as the percentage of dropping samples in which this group was found). For statistical analyses, insect prey items were categorized into seven groups: (1) Arachnida – spiders and harvestmen; (2) Scarabaeoidea larvae – larval stages of scarabaeid beetles; (3) Other Coleoptera – all beetles of all developmental stages with the exception of previous category; (4) Lepidoptera – butterflies and moths of all developmental stages; (5) Orthoptera – grasshoppers and crickets; (6) Other taxa – all other invertebrates; and (7) Unidentified prey items. The taxonomic nomenclature was used and prey taxa were arranged according to de Jong (2013).

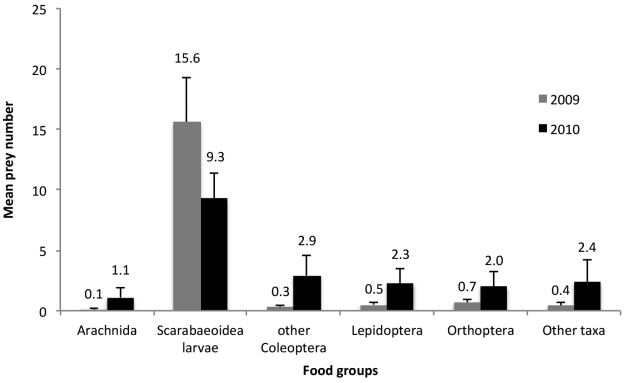


Fig. 2. Interannual comparison of mean prey numbers of the six food groups in the same nestboxes (n = 11) obtained by camera recordings (given are mean and SE for each food group).

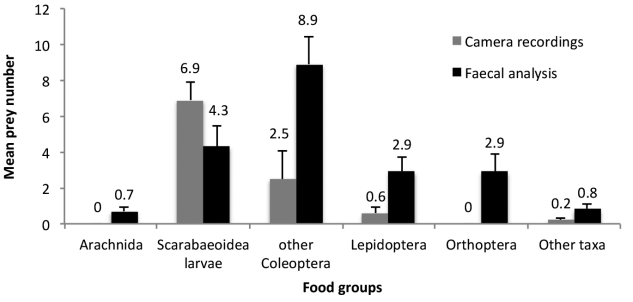


Fig. 3. The comparison of mean prey numbers of the six food groups in the same nests (n = 10) in 2010 obtained by two methods (given are mean and SE for each food group).

Results

Diet composition of hoopoe nestlings in vineyard habitats

Including both years and sample techniques, 1214 prey items were collected and 1081 of them were classified into 90 species, 32 families and 11 orders of invertebrates (see Table 1). The total species number estimate was based on identified species and approximate species number in higher taxa. In the camera recordings, we have been able to identify 608 of 741 prey items (82.0 % of all items). Based on the dominance of the identified prey items only, we found scarabaeid larvae to be the most dominant prey (73.4 % of identified items). The remaining prey groups including "other beetles" (8.1 %), butterflies and moths (5.9 %), orthopterans (4.9 %), spiders and harvestmen (2.3 %) are by far less abundant in the diet of hoopoe nestlings. Each of the smaller arthropods

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Table 2. The most important taxa in the food of the hoopoe (n% only in identified prey taxa), comparison of formerly published and our data. Explanations: n = abundance, n% = dominance.

Auhor	Own data		Krištín 1993		Fournier & Arlettaz 2001		Stange & Havelka 2003		Pühringer 2008		Rieder & Schulze 2010		Arlettaz et al. 2010	
Country/ habitat	Lower Austria/ vineyards		Slovakia/ oak pastures		Switzerland/ mosaic agricultural plain		Germany/ vineyards		Upper Austria/ pastures, orchards		Austria/ agricultural landscape		Switzerland/ mosaic agricultural plain	
Food taxa	n	n%	n	n%	n	n%	n	n%	n	n%	n	n%	n	n%
Arachnida	43	4.0			80	2.3								
Scarabaeoidea larvae	541	50.0	207	27.9	25	0.7					338	83.7		
other Coleoptera	245	22.7	115	15.5	33	0.9	44	39.6			3	0.7		
Lepidoptera	93	8.6	50	6.7	2349	67.3							1091	23.8
Gryllotalpa gryllotalpa			3	0.4	892	25.5	36	32.4	10	31.3	63	15.6	3218	70.2
other Orthoptera	93	8.6	299	40.3	4	0.3			2	6.2				
Other taxa	66	6.1	68	9.2	59	1.7	31	28	6	18.8			273	6.0
Unidentified larvae					25	0.7			14	43.7				
Podarcis muralis					26	0.7								
Unidentified prey items	133				42		8						872	
Total no. of prey items	1214	100	742	100	3535	100	119	100	32	100	404	100	5454	100

like flies Diptera, hymenopterans Hymenoptera, earwigs *Forficula auricularia* and earthworms Lumbricidae made up less than 1 % and comprise together 5.4 % in the group "other taxa".

In faecal samples, we found in total 473 prey items, on average 5.6 ± 0.3 per sample. In contrast to the camera recordings, the most dominant prey was the group "other beetles" (41.4 %). Scarabaeid larvae have been identified only in 20.1 % of all items. Orthopterans (13.3 %), butterflies and moths (12.1 %), and spiders and harvestmen (6.1 %) were less dominant but more abundant than in camera recordings. "Other taxa" including flies, hymenopterans, earwigs, heteropterans Heteroptera and lacewings Neuroptera represented 6.9 % of the prey. Regarding the frequency of prey taxa (including taxa we were not able to count), the most frequent taxa were scarabaeid larvae (73.8 %), followed by butterflies and moths (65.5 %), ground beetles Carabidae (63.1 %) and earthworms (58.3 %).

Interannual variation in diet composition

Comparing the numbers of prey items in each of the six identified prey groups obtained by camera recordings in the same 11 nestboxes between two sampling years, we found no significant difference in any of the prey groups: scarabaeid larvae (paired sample t-test: $t = 1.757$, $p = 0.109$), orthopterans ($t = 1.068$, $p = 0.311$), butterflies and moths ($t = 1.715$, $p = 0.117$), "other beetles" (Wilcoxon's signed-ranks test: $T = 28.0$, $p > 0.05$), spiders and harvestmen ($T = 21.0$, $p > 0.05$), and the group "other taxa" ($T = 28.0$, $p > 0.05$) (Fig. 2).

Differences in diet composition obtained by two sampling techniques

Comparing the number of items in the six identified prey groups in the same 10 nests as obtained by two sampling methods, we found significant differences in four categories: orthopterans (paired sample t-test: $t = 3.022$, $p = 0.014$), "other beetles" ($t = 3.588$, $p = 0.006$), spiders and harvestmen ($t = 2.689$, $p = 0.025$) and the group lepidopterans ($t = 2.274$, $p = 0.049$). The group "other beetles" was most different, whereas the two remaining groups did not differ: "other taxa" ($t = 1.616$, $p = 0.140$) and scarabaeid larvae ($t = 1.292$, $p = 0.228$) (Fig. 3).

Furthermore, we found a significant difference in the size of prey items in faecal samples and in camera recordings. The average prey size of the faecal samples (18.2 ± 0.5 mm) was significantly smaller than that in the camera recordings, (22.9 ± 0.6 mm) (Mann-Whitney U-test: $Z = 3.463$, $p < 0.001$). In faeces, we found a significantly different taxon diversity ($H' = 2.756$) than in camera recordings ($H' = 1.170$) ($t = 10.852$, $p < 0.001$).

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Discussion

Similar to findings in other habitats across the European breeding range, we found that our vineyard hoopoe population prefers larger arthropods and their ground-inhabiting larvae (Table 2). Although the hoopoe is opportunistic regarding to food choice (Rieder & Schulze 2010), the dietary range of the nestlings in our population appears to be quite narrow. The main components of the diet in vineyards were beetles, in particular ground-dwelling scarabaeid larvae (see also Bussmann 1950, Hirschfeld & Hirschfeld 1973, Krištín 1993, Stange & Havelka 2003, Rieder & Schulze 2010). Comparably, the majority of studies referred to large prey like cockchafer larvae or molecrickets *Gryllotalpa gryllotalpa* (Table 2). However, less information is available on smaller prey (some findings are reviewed in Münch 1952, Hirschfeld & Hirschfeld 1973, Glutz von Blotzheim & Bauer 1994, Krištín 2001). Small prey can become important, when large food is not available or less abundant (Hoi et al. 2004). For example, using neck-collars, Hirschfeld & Hirschfeld (1973) identified also smaller prey items under 12 mm, e.g. *Stenobothrus lineatus* (1 ex.), *Tipula* sp. (1 ex.) or *Lycosa* sp. (12 ex.) and Stange & Havelka (2003) found 24.7 % of Syrphidae larvae in two hoopoe broods. According to 32 photographs of the prey provisioned to hoopoe nestlings in Upper Austria, Tipulidae larvae (3 ex.) and *Eristalis* sp. larvae (1 ex.) were identified (Pühringer 2008). Fournier & Arlettaz (2001) identified also fly larvae (12 ex.) and rarely ants Formicidae (1 ex.) in seven hoopoe broods in Switzerland. However, less is known about smaller beetles, especially about coprophagous scarabaeids or zoophagous small carabids in the hoopoe diet. Our results revealed that hoopoe parents fed their nestlings also with small scarabaeid beetles *Onthophagus* sp. (44 ex.), *Aphodius* sp. (3 ex.), and *Geotrupes* sp. (11 ex.), as well as with species typical for a sandy environment, e.g. ant-lion larvae Myrmeleonidae (11 ex.) (review also in Glutz von Blotzheim & Bauer 1994), earwigs (18 ex.), or faster-moving carabids like *Pterostichus* sp. (13 ex.) and larger *Carabus* sp. (36 ex.). We did not find any molecrickets in our study, although this prey is considered the main component of hoopoe diet in some other studies (Table 2). Hence, we can conclude that molecrickets are not always a major compound of hoopoe diet and that hoopoe nestling diet is on one hand opportunistic but on the other hand quite narrow (Fournier & Arlettaz 2001, Barbaro et al. 2008, Rieder & Schulze 2010). This might to have to do with the fact that available prey frequently appears ephemeral in particular microhabitats where hoopoes forage preferentially. Given these typical diet features, one would also expect interanual variation in diet composition.

Rainy periods have shown to have negative effect on foraging whereas seasonal droughts can strongly increase juvenile survival in hoopoe populations (Arlettaz et al. 2010). When raining for example, insect larvae may hide in deeper soil layers (Goodyer & Nicholas 2007) and climatic or soil conditions are the factors responsible for the survival of hoopoes' main prey – ground dwelling scarabaeid larvae (Zweigelt 1928). Consequently, although we expected that rainy weather in 2010 will affect the composition of prey delivered to hoopoe nestlings, we did not find any significant difference between 2009 and 2010. In both years, parents provisioned their nestlings with large scarabaeid larvae, which suggest their highly specialized hunting skills on soil-dwelling insects. Large larvae were available especially on the bare ground between vine trunks (own unpublished results). The bare ground (mainly unploughed) is generally crucial for feeding of several declining ground foraging insectivorous farmland bird species (Romanowski & Żmihorski 2008, Hoste-Danylow et al. 2010, Schaub et al. 2010, Thorup et al. 2010, Tagmann-Ioset et al. 2012).

Beside temperature and rainfall there is a number of factors that could influence food composition as well, e.g. the diet provisioned to offspring can be affected by ambient current conditions. Also sampling at different times of the year or the phenology of the prey for the offspring are crucial factors for diet composition, e.g. in years with cockchafer outbreaks, the diet composition of birds can significantly depend on multi-annual cycles of this beetle (Krištín 1993, Hoi et al. 2004). In this context also the timing of breeding and abundance of insects as optimal food can be a main selection pressure for many insectivorous birds (Visser et al. 2006). Seasonal changes of the prey availability during the breeding season also affect the diet composition of merlin (*Falco columbarius*) nestlings (Fernández-Bellon & Lusby 2011). In conclusion, we believe that, for hoopoes, the vineyard comprises a habitat that provides stable conditions for prey diversity among the years.

However, variability in the diet composition could be also due to different sampling techniques. In this context our camera recordings revealed significantly larger prey items than found in faecal samples. Additionally the two sampling methods revealed significant differences in four out of six prey groups

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compared in the same nestboxes (see results). Thus, the extreme bias towards big prey could be to some degree related to the visual sampling method. The existence of smaller prey items mainly found in faecal samples is novel. Additionally in faecal samples, we further found a significantly higher diversity of arthropods than in camera recordings (see results and Table 1). Although both methods have shown a high abundance of the two groups of Coleoptera ("Scarabaeoidea larvae" and "other Coleoptera"), the biggest difference was found in the group "other Coleoptera" (see Fig. 3). We assume that the small sclerotized prey items hard to digest were easier to detect in faecal samples than the respective prey in the camera recordings, which could be also the reason for the significant difference in the abundance of "other Coleoptera".

On the other hand, to determine the abundance of soft-bodied prey items in faeces can be problematic, e.g. the estimation of earthworms' chaetae (Kleintjes & Dahlsten 1992, Scheiffarth 2001, Hounsome et al. 2004, Obuch & Krištín 2004). However, an increased consumption of earthworms might occur only when the usual prey is not available (e.g. observed in common buzzards and little owls, see Hounsome et al. 2004). In fact the significant differences in the four groups were mainly due to smaller prey (e.g. arachnids) or prey with sclerotized body parts (e.g. orthopterans, beetles). These prey taxa are often processed by hoopoes into pieces and so they cannot be identified in camera recordings. Still, the frequency of large, but soft-bodied arthropods (scarabaeid larvae) or some species that were included in the group "other taxa" did not differ, which confirms a strong dependence on large prey (larvae) for our model species or a relatively good resolution of specific taxa (e.g. *Forficula auricularia* or Diptera items) in both methods.

The most striking difference we found in relation to others studies was related to the occurrence of earthworms. The frequency of taxa identified in faeces showed that remnants of earthworms were found in more than the half of all faecal samples. This finding is however not consistent with our camera results (only one specimen was found in 2010, Table 1) and with findings of earlier studies. For example, it has been shown that within 247 food items of a hoopoe diet in Moldavia, only two earthworms were found (Glutz von Blotzheim & Bauer 1994). Similarly, in 3493 identified prey items, Fournier & Arlettaz (2001) found only 0.5 % of earthworms in an agricultural plain with small patches of trees and orchards. Several studies have not even mentioned the presence of earthworms in the hoopoe diet (Krištín 1993, dry oak pastures; Stange & Havelka 2003, vineyards; Pühringer 2008, pastures, orchards and meadows; Arlettaz et al. 2010, agricultural plain with small patches of trees and orchards; Rieder & Schulze 2010, agricultural landscape). Thus, our results suggest that in contrast to earlier findings based on mainly visual methods, earthworms might be more common in the hoopoe prey. We think that hoopoe parents feed their young with earthworms, especially during rainy days, because hoopoes are generally opportunistic and earthworms are an easy prey at that time. A further methodical problem of camera recordings that should be mentioned here is that camera recordings are usually restricted to periods of dry weather. On the other hand, the higher frequency of stiff hairs in faeces may be an overestimate, chaetae could have been intercepted into an epithelium of a digestive system and might therefore be repeatedly released into faecal samples during digestion, or they could come from the digestive system of other hoopoe prey such as predatory beetles (Z. Šustek, pers. comm.). Thus, the real frequency of earthworms in the hoopoe can be overestimated in faecal samples.

In conclusion, our results revealed some novel aspects regarding hoopoe food intake and nestling diet, particularly regarding variability and sampling techniques. The results can have important implications for conservation actions, considering the high intake of ground dwelling insects and ground-inhabiting larvae. These prey taxa prefer mosaic habitat patterns of grassland and bare ground with a species-specific bare ground coverage of 30-70 % (Schaub et al. 2010, Arlettaz et al. 2012). One suggestion of our study would be to implement patches of bare ground throughout vineyards in order to prevent further decline of insectivorous ground foraging farmland birds.

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