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Food provision to nestlings in the Hoopoe *Upupa epops*: implications for the conservation of a small endangered population in the Swiss Alps

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In an attempt to recognize the possible ecological causes of the decline of a population of Hoopoes *Upupa epops* in the Swiss Alps, we collected data on resource exploitation. The prey provisioned to nestlings by parents was investigated at four breeding sites using photographs (n = 4353, 80% of which enabled prey identification). Molecrickets *Gryllotalpa gryllotalpa* and Lepidoptera (larvae and pupae) were dominant in nestling diet (93% frequency; 97% biomass). Although Molecrickets were provisioned less frequently (26%) than Lepidoptera (67%), they represented 68% of the total biomass (vs 29% for Lepidoptera). There was an overall negative relationship between the proportion of Molecricket biomass in the diet and the parents' feeding rate, whereas a comparison between broods showed that a higher provisioning activity did not lead to an increase in the biomass supplied to the chicks. A diet based on Molecrickets therefore appears to be energetically advantageous. As Molecrickets are a traditional prey of Hoopoes in central Europe, this might be relevant to other populations. In the study area, Molecrickets occur only on the intensively cultivated plain, whereas the majority of Hoopoe pairs nest at various altitudes on the foothills adjacent to the plain as the latter provides at present almost no suitable nesting sites. Hoopoes breeding higher up on the foothills seem to experience greater provisioning costs and have, on average, lower breeding success. Providing nest sites on the plain is the main conservation measure proposed for the local Hoopoe population. Further attention should also be paid to Molecrickets as these may be crucial for Hoopoes.

As a typical inhabitant of traditionally cultivated landscapes, the Hoopoe is at present considered as one of the most endangered bird species in western and central Europe (Hustings 1997). This contrasts with its status around the Mediterranean – and to a lesser extent in eastern Europe – where the Hoopoe is a common and widespread bird in agricultural areas (Rehsteiner 1996). The unequal status of Hoopoe populations across Europe probably mirrors the degree of intensification of farming practices.

In Switzerland, breeding pairs are now essentially confined to the southwest, with a stronghold in Valais (Praz 1980). Even in Valais, however, regular censuses carried out over 12 years (1978–89) have shown a slow but progressive reduction of the breeding area (Arlettaz & Fournier 1989). In an attempt to identify the reasons for this recent decline, we studied resource exploitation by Hoopoes in a small population in Valais. In particular, we investigated the food provisioned to nestlings by parents with respect to nest-site location and the habitat of origin of the main prey. We related these data to the overall reproductive performance. From this, some recommendations can be proposed for the conservation of this local population, which may be relevant to other populations.

STUDY AREA AND METHODS

Study area and Hoopoe population

This study was carried out in the canton of Valais, in

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the Upper Rhône valley, in the southwestern Swiss Alps (46°07′N, 07°08′E). Landscape, climate and vegetation have been described by Arlettaz (1984) and Fournier (1991). Since the 1950s and 1960s, the plain (460–468 m asl) is almost exclusively devoted to industrial farming, mostly orchards with small trees, with only three remnants of woodlands at the eastern end of the study area. The lowest parts of the adjacent south-exposed slope are extensively covered by vineyards, but patches of natural habitat, including steppe grassland and xeric deciduous forests, also remain (see photographs in Arlettaz 1984). Human settlements extend along the contact zone between the slope and the plain. The majority of Hoopoes breed in tree holes in forests on the slope, mostly at forest edges, although much of their feeding activity takes place on the neighbouring plain (Arlettaz 1984, this study). In the study area, 12 breeding pairs were found in 1982. However, the number of nests precisely located was eight in both 1982 and 1983 (Arlettaz 1984). The population seems even smaller today, but there are no precise figures for population size since the 1980s (Arlettaz & Fournier 1989).

Nestling diet

The prey spectrum brought to the nestlings by their parents was recorded by cameras, as described by Royama (1959). Seven broods were surveyed at four breeding sites (situated at 468, 500, 510 and 700 m asl, respectively) in 1989 and 1990 (Appendix 1), but 1989 was a test year. Despite considerable effort, we could find only six breeding cavities in 1989 and four in 1990. We believe that the entire breeding population was surveyed using cameras in 1990, the year in which most of the work was done. A total of 4353 slides showing feeding adults was collected over 59 days. The cameras were hidden in wooden boxes installed about 1.5–2 m from the nests; the boxes were fixed on a neighbouring tree, wall, or placed on the ground. Similar equipment was used in studies on Little Owls *Athene noctua* and Scops Owls *Otus scops* (Juillard 1983, 1984, Arlettaz *et al.* 1991). The cameras (Contax RTS) were equipped with a motor drive and 80–210 mm lens, and were triggered when the adults crossed an infrared light beam positioned around the nest entrance. Because Hoopoes bring only one item at a time while feeding chicks, identification of prey was usually easy, although not always possible due to the position of the bird's bill. Cameras were equipped with backs that offered an extended capacity allowing the use of 250-exposure films to cope with the high frequency of food provisioning. We used 64 ASA slide films (Ektachrome, Kodak). Film rolls of about 250 exposures were prepared in a dark room from the 30-m long original films supplied by Kodak. In poor light conditions, flash light had to be used, which did not seem to disturb the birds. The aperture was set at f 8.0 and shutter speed at 1/60 s. Power supply for both the camera and flash was provided by 12 V car batteries. Close to the nest entrance, we placed a clock which was visible on the photographs.

Prey were identified according to Aspöck *et al.* (1980), Balachowsky and Mesnil (1936), Chinery (1988), Galet (1982), Grandi (1984) and Jones (1990).

Estimation of prey biomass

The dry biomass of the prey items was estimated using data from a study on bats by Arlettaz and Perrin (1995, Appendix 2). These authors sampled ground- and grass-dwelling arthropods in intensively cultivated orchards on the plain of the Rhône, about 5 km from the study area, as well as on xeric slopes covered by steppe vegetation within our study area. Both habitats are typical Hoopoe foraging grounds (Arlettaz 1984). Arthropods collected in the field were stored in 70% ethanol in small plastic bags, dried for 72 h at 65°C (Arlettaz & Perrin 1995). For this study, the dry weight of the various prey was measured to the nearest 0.01 g using a precision balance (Mettler-Toledo BD 202, Greifensee, Switzerland). A single average biomass value was obtained for each prey taxon that did not show much size variation. For Molecrickets *Gryllotalpa gryllotalpa*, however, we were able to distinguish six size categories, and a specific biomass value was attributed to each of them.

Origin of prey

We attempted to locate the habitats where parents collected food, using 10× or 25× magnification binoculars. This could be achieved for two nests (i.e. half of the nests available in 1990) on the south-exposed slope above the plain, where vantage points enabled an almost continuous survey of the parents' movements between the nest and their foraging grounds on the plain. In contrast, such data could not be collected for the pairs nesting and foraging on the plain. The time of departure from and arrival at the nest was recorded while watching the movements of the birds. By matching these data with the photographs of provisioning adults, we could estimate where a given prey item was captured.

Reproductive success vs nest location

The number of young fledged was recorded for as many nests as possible between 1979 and 1998. Data collected at the same site over successive years were considered to be independent since there was a high probability that they were inhabited by several adults over such a long period of time. Inaccessible cavities were checked using a small mirror placed on a flexible plastic stick with a bulb fixed at the extremity of two electric leads connected to a 4.5 V battery (Fournier 1991). Yet, even using this method, the exact content of many cavities remained unknown.

RESULTS

Diet of nestlings

Table 1 summarizes the data, nest by nest. A total of 3493 prey items could be identified (80%) from 4353 slides; 19% of prey items were not clearly visible. One per cent of prey items was clearly visible on the pictures but could not be attributed to a specific prey category.

The two dominant prey categories were Molecrickets (mostly adults and large larvae) and Lepidoptera, accounting for 93% of all prey items and 97% of the overall estimated prey biomass (henceforth referred to as biomass). All other prey types were marginal, each representing < 2.5% of the overall frequency and biomass. Lepidoptera consisted mainly of caterpillars, which were seven times more abundant

Table 1. Absolute (*N*) and relative (%) number of prey items, and estimated dry biomass (%) provisioned to nestlings by parent Hoopoes at four different breeding sites (seven broods). The number of days with photographic coverage is given.

	Site A									Site B		
	1989, 1st brood 3 days			1990, 1st brood 9 days			1990, 2nd brood 7 days			1990, 1st brood 14 days		
	Frequency		Mass	Frequency		Mass	Frequency		Mass	Frequency		Mass
	N	%	%	*N*	%	%	*N*	%	%	*N*	%	%
Annelida (*Lumbricus* sp.)	3	1.3	4.8	11	0.9	3.1	2	1.0	1.5	0	0	0
Mollusca (*Arion ater*)	0	0	0	0	0	0	0	0	0	0	0	0
Araneidae	8	3.6	1.7	54	4.6	2.0	4	2.1	0.4	3	0.4	0.1
Diplopoda (Iulidae)	1	0.5	0.4	1	0.1	0.1	0	0	0	0	0	0
G. gryllotalpa	10	4.5	25.4	93	7.8	34.6	84	43.3	81.9	342	48.5	86.4
G. campestris	0	0	0	0	0	0	0	0	0	0	0	0
Acrididae (larvae)	0	0	0	1	0.1	0	0	0	0	0	0	0
Mantis religiosa (larvae)	0	0	0	1	0.1	0	0	0	0	0	0	0
Heteroptera	0	0	0	2	0.2	0	0	0	0	0	0	0
Libelluloides sp. (larvae)	0	0	0	4	0.3	0.1	15	7.7	0.9	0	0	0
Lepidoptera (larvae)	173	78.2	58.4	890	75.0	52.0	77	39.7	12.3	354	50.2	13.3
Lepidoptera (pupae)	0	0	0	59	5.0	3.9	7	3.6	1.3	1	0.1	0.1
Lepidoptera (imagos)	0	0	0	0	0	0	1	0.5	0.1	0	0	0
Diptera (larvae)	1	0.5	0.1	9	0.8	0.1	0	0	0	0	0	0
Formicidae	0	0	0	0	0	0	0	0	0	0	0	0
Other Hymenoptera	0	0	0	1	0.1	0	0	0	0	0	0	0
Scarabaeidae (larvae)	24	10.8	9.1	1	0.1	0.1	0	0	0	0	0	0
Other Coleoptera (larvae)	0	0	0	11	0.9	0.2	1	0.5	0.1	2	0.3	0.1
Coleoptera (imagos)	1	0.5	0.2	10	0.8	0.3	0	0	0	2	0.3	0.1
Unidentified larvae	0	0	–	16	1.3	–	1	0.5	–	0	0	–
Podarcis muralis	0	0	0	0	0	0	1	0.5	1.1	0	0	0
Podarcis muralis (eggs)	0	0	0	23	1.9	3.5	1	0.5	0.4	1	0.1	0.1
Total identified prey	221	100	100	1187	100	100	194	100	100	705	100	100
Unidentified prey items	5			21			1			5		
Prey not visible on slides	96			318			12			298		
Total provisioned prey	322			1526			207			1008		

continued

than pupae, and we found only one imago. Although Molecrickets represented only 26% of all provisioned prey, their biomass amounted to 68% of the total. By contrast, Lepidoptera, with 67% of the number of prey brought to the nests, made up only 29% of the overall biomass (Appendix 2).

There was some variation within and between broods in the relative importance of these two prey categories. At site A (upper foothill), the biomass of Lepidoptera (58% and 56%, in 1989 and for the first brood in 1990, respectively) was greater than in *G. gryllotalpa* (25 and 35%). However, at the same site A in 1990 (second brood), as well as for all other broods investigated (lower foothill and plain), Molecrickets were always the most important prey biomass, ranging from 54% (site C) to 92% (site B, second brood).

Food provisioning and foraging habitat

Feeding rate

There were no distinctive time (between hours) patterns in food provisioning by parent Hoopoes during the day (Kruskal–Wallis analysis of variance, $KW_{14} = 4.488$, $P = 0.99$; Fig. 1), but considerable daily variation within and between broods among five broods for which continuous daily photographic monitoring was obtained (n = 17 days). We therefore also consider broods with days of incomplete photographic coverage (but with > 200 min of continuous data), and compare the hourly provisioning activity between the different breeding situations.

Figure 2 shows the mean number of feedings per hour of the incubating female by the male (site B, second brood in 1990) and of the chicks by their

Table 1 continued.

	Site B			Site C			Site D			All sites together		
	1990, 2nd brood 13 days			1990, 2nd brood 10 days			1990, 1st brood 3 days			7 broods 59 days		
	Frequency		Mass	Frequency		Mass	Frequency		Mass	Frequency		Mass
	N	%	%	*N*	%	%	*N*	%	%	*N*	%	%
Annelidae (*Lumbricus* sp.)	2	0.7	0.8	0	0	0	1	0.8	1.3	19	0.5	1.1
Mollusca (*Arion ater*)	0	0	0	1	0.1	0.2	0	0	0	1	0.1	0
Aranaeidea	7	2.5	0.3	4	0.5	0.2	0	0	0	80	2.3	0.6
Diplopoda (Iulidae)	0	0	0	1	0.1	0.1	0	0	0	3	0.1	0
G. gryllotalpa	186	65.7	91.8	131	17.0	54.0	46	35.1	76.8	892	25.5	68.1
G. campestris	1	0.4	0.2	0	0	0	0	0	0	1	0.1	0
Acrididae (larvae)	1	0.4	0	0	0	0	0	0	0	2	0.1	0
Mantis religiosa (larvae)	0	0	0	0	0	0	0	0	0	1	0.1	0
Heteroptera	0	0	0	1	0.1	0	0	0	0	3	0.1	0
Libelluloides sp. (larvae)	0	0	0	0	0	0	0	0	0	19	0.5	0.1
Lepidoptera (larvae)	67	23.7	5.4	423	54.8	29.7	83	63.4	21.9	2067	59.2	24.8
Lepidoptera (pupae)	15	5.3	1.3	199	25.8	15.7	0	0	0	281	8.0	3.8
Lepidoptera (imagos)	0	0	0	0	0	0	0	0	0	1	0.1	0
Diptera (larvae)	0	0	0	2	0.3	0	0	0	0	12	0.3	0
Formicidae	0	0	0	1	0.1	0	0	0	0	1	0.1	0
Other Hymenoptera	0	0	0	0	0	0	0	0	0	1	0.1	0
Scarabaeidae (larvae)	0	0	0	0	0	0	0	0	0	25	0.7	0.3
Other Coleoptera (larvae)	4	1.4	0.1	1	0.1	0	0	0	0	19	0.5	0.1
Coleoptera (imagos)	0	0	0	1	0.1	0	0	0	0	14	0.4	0.1
Unidentified larvae	0	0	–	7	0.9	–	1	0.8	–	25	0.7	–
Podarcis muralis	0	0	0	0	0	0	0	0	0	1	0.1	0.1
Podarcis muralis (eggs)	0	0	0	0	0	0	0	0	0	25	0.7	0.8
Total identified prey	283	100	100	772	100	100	131	100	100	3493	100	100
Unidentified prey items	1			6			3			42		
Prey not visible on slides	3			84			7			818		
Total provisioned prey	287			862			141			4353		

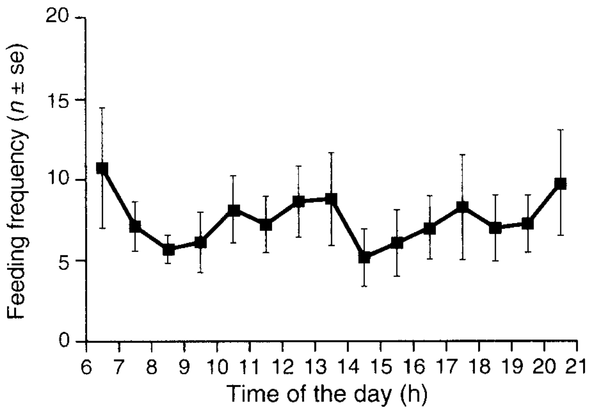

Figure 1. Average (± 1 se) chick feeding frequency per hour in five broods at three different breeding sites. Standard errors show the among-brood variation.

parents for four broods, excluding days with < 200 min of total photographic monitoring. Feeding activity peaked about 8–24 days after hatching of the first egg. Note that food provisioning was more frequent at the highest site (700 m asl; Appendix 1). Chick feeding activity was apparently particularly low for the second brood at site B.

Provisioned biomass vs feeding rate

There was no overall significant relationship between the biomass brought to the nest and the feeding frequency of parents at chick age 8–24 days (Spearman rank correlation, $r_s = 0.393$, $n = 7$, ns) – note that to avoid pseudoreplication, tests were performed on mean brood values (Fig. 3). This suggests that a higher feeding rate (if we roughly compare the different breeding sites) did not lead to a higher biomass supplied to the nestlings (but note the intra-brood trends in Fig. 3a). In contrast, there was a strong negative relationship between the mean prey item biomass and the hourly feeding rate ($r_s = -0.821$, $n = 7$, $P < 0.05$; Fig. 3b). Correspondingly, as Molecrickets are clearly the heaviest prey, there is a negative relationship between the proportion of this prey in the biomass provided to the brood and feeding rate ($r_s = -0.964$, $n = 7$, $P < 0.01$; Fig. 3c).

Habitat of the main prey

Table 2 shows the probable habitat of origin of 141 prey items brought to two sites. At least 93% of Molecrickets came from the plain, whereas almost all Lepidoptera larvae (98%) and pupae (100%) were captured on the foothill. The remaining 7% of Molecrickets were certainly also captured on the plain, but the returning parents were not detected prior to flying above vineyards (i.e. on the foothill) so that prey origin was conservatively attributed to the foothill. Further observations have established that, in the study area, *G. gryllotalpa* is found exclusively on the plain but is absent on the rocky soils on the south-exposed foothill (Arlettaz and Perrin 1995).

Breeding success and nest location

The site on the upper foothill yielded four fledglings per breeding attempt ($n = 3$), whereas all other

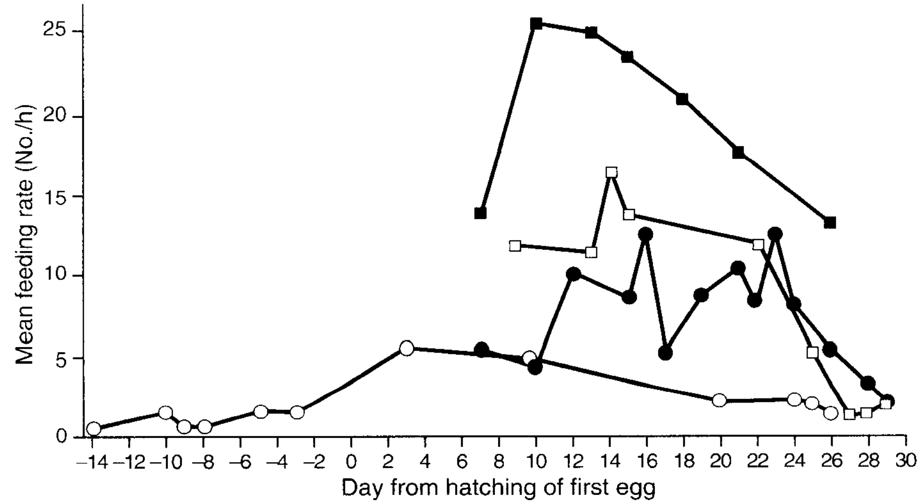

Figure 2. Mean feeding rate per hour at different stages of the breeding cycle (0 = hatching day of the first egg) at four broods with adequate photographic coverage. ■, Site A 1990, first brood, 700 m; ●, site B 1990, first brood, 510 m; ○, site B 1990, second brood, 510 m; □, site C 1990, second brood, 468 m.

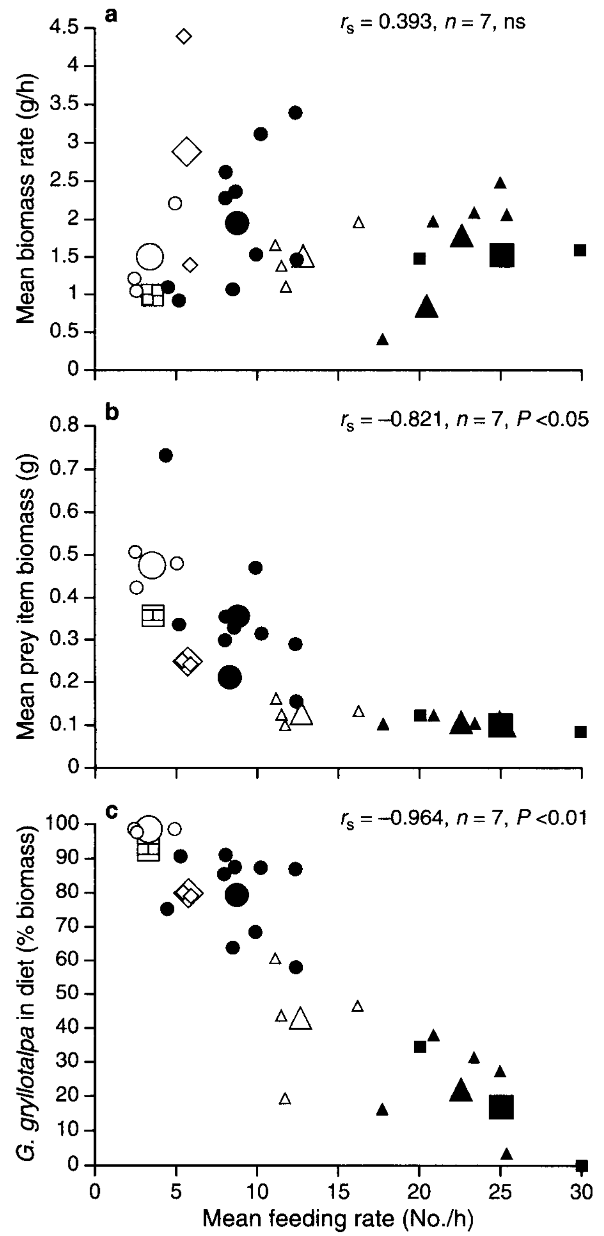

Figure 3. Biomass and percentage of Molecrickets in the diet plotted against parental feeding rate (mean per hour) for seven broods. Each brood is represented by a different symbol. Small symbols correspond to data collected on one day, large symbols represent mean brood values. (a) Mean absolute biomass provisioned per hour (g/h) vs mean feeding rate per hour. (b) Mean prey item biomass (g) vs mean feeding rate per hour. (c) Percentage of Molecricket biomass in diet vs mean feeding rate. The tests were performed on mean values.

Table 2. Local geographic origin of prey items provisioned to nestlings (*n* = 141) at sites A and B.

	Foothill (slope)		Plain	
	N	%	*N*	%
Aranaeidea	3	100	–	–
G. gryllotalpa	4	7.3	51	92.7
Libelluloides sp. (larvae)	1	–	–	–
Lepidoptera (larvae)	60	98.4	1	1.6
Lepidoptera (pupae)	13	100	–	–
Diptera (larvae)	1	–	–	–
Formicidae	1	–	–	–
Other Coleoptera (larvae)	3	–	–	–
Coleoptera (imagos)	1	–	–	–
Podarcis muralis (eggs)	1	–	–	–
Total	89	52		

breeding sites on the lower foothill or on the plain gave five fledglings each ($n = 4$; Appendix 1). Furthermore, although a large variation in clutch size renders inter-site comparisons risky, it is noteworthy that chick mortality is apparently associated with a low proportion of Molecrickets in the diet. At site A in 1989 and for the first brood in 1990, where Molecrickets accounted for only 25 and 35%, respectively, of biomass in the diet, chick mortality was 33% and 43%. In all other cases, including a second brood at site A in 1990, where Molecricket biomass exceeded 54%, all chicks fledged.

To test further whether breeding performance was related to nest altitude, we attempted to use all data on breeding success since the late 1970s, although no extensive information on diet composition existed for most of that period. Data on breeding success were plotted against nest-site altitude. If it is true that Molecrickets have a positive influence on breeding performance, there should be a negative relationship between number of fledglings and nest altitude, because Molecrickets occur only on the plain. We found a significant decrease in the number of fledglings per brood with increasing altitude ($r_s = -0.463$, $n = 42$, $P < 0.005$).

DISCUSSION

Although Hoopoes in the study area were able to capture a wide variety of prey, from slugs and earthworms to insects and lizards, nestling diet appeared quite specific. Molecrickets and Lepidoptera larvae and pupae were the most important food source, with 68% and 29% of the estimated overall biomass, respectively. Although there are no other comprehensive studies on nestling diet in this species, our study confirms former findings that Lepidoptera larvae and pupae, and underground-dwelling prey such as

Molecrickets, are typical prey of Hoopoes (e.g. Csiki 1905, Bussmann 1950, Riabov 1965, Gania *et al.* 1969, Hirschfeld & Hirschfeld 1973). The importance of Molecrickets in the diet has already been described from observation by Stirnemann (1940, 1941, 1943, 1948), Aellen (1942), Bussmann (1950), Creutz (1951), Heldmann (1951), Ammersbach (1952), Gerber (1960) and Arlettaz (1982). Stirnemann (1940), Aellen (1942) and Heldmann (1951) further estimated that this prey may account for up to 80–100% of diet. The occurrence of Molecrickets might therefore be crucial for the survival of Hoopoe populations in central Europe.

It may be argued that the low diet diversity observed in our nestling Hoopoes might result from the progressive impoverishment of the arthropod fauna, as a consequence of the recent agricultural intensification. For example, larval scarabaeid beetles, which live underground, appeared far less frequently in our nestling diets than in earlier studies (e.g. Csiki 1905, Gania *et al.* 1969), and this may be because most scarabaeid species such as Cockchafers *Melolontha melolontha* are locally extinct due to the destruction of pastureland and hay meadows on the plain, and to the widespread use of insecticides in intensively cultivated orchards. The same would apply to Lepidoptera larvae which have become extremely rare on the plain. In the absence of comparable dietary studies in areas with high Hoopoe densities, it is difficult to draw conclusions, although old data by Stirnemann (1940), Aellen (1942) and Heldmann (1951) support the hypothesis of diet specialization in the Hoopoe.

Could the local population of Hoopoes survive without available Molecrickets? In the study area, this large prey certainly presents the best option where it occurs (Table 2). The importance of Molecrickets in the present context seems to be supported by breeding performance, since chick mortality was greater when the proportion of that prey in the diet was low, and at higher altitudes. However, large trees sheltering natural breeding cavities (usually woodpecker holes) have mostly been eliminated from the plain (where Molecrickets occur), except for three remnants of forest, each of which is occupied by a pair of Hoopoes. Hoopoes are therefore forced to seek cavities on the adjacent foothills. There, they use either natural sites, mostly holes excavated by woodpeckers in old chestnut or oak trees, or, less frequently, niches within walls supporting vineyard terraces. A clear consequence of this is that birds must travel further than in the past to feed on the good areas on the plain. Provisioning efficiency would therefore be reduced for most breeding pairs, and this might have been involved in the population's decline. In our opinion, although our sample is small, this scenario is exemplified by the site most remote from the plain which was investigated photographically (site A, 700 m altitude, i.e. 240 m above the plain). There, chick feeding activity was far greater than at the other breeding places (Figs 2 & 3) and both parents mainly captured small items with a low prey profitability. In this case, it seems that a higher feeding frequency was necessary to supply sufficient biomass for chick development (Fig. 3a); in other words, parents presumably compensated for the excessively low prey profitability by increasing their feeding rate. We do not know the consequences of this for adult survival.

It would be wrong, however, to assume that finding a cavity on the plain is sufficient for optimal breeding. As indicated by site C, breeding success would benefit further from nesting close to dense populations of Molecrickets on the plain itself. Located in one of the remaining forest fragments on the plain, site C is surrounded by gravelly soils which are not particularly suitable for Molecrickets that prefer softer ground. Fewer Molecrickets (54% of biomass) were therefore brought by this pair, which also had a relatively high feeding frequency (Figs 2 & 3). The average breeding performance of this pair might be explained by the energetically less demanding commuting flights within the plain itself, as opposed to the flights from low to high elevations along the foothill slope experienced by birds at site A.

Clearly, Hoopoe survival in the area might be ensured by improving the natural breeding performance of the few remaining pairs by creating nesting sites on the plain. In the long term, this requires planting hedges or woodlands which would attract woodpeckers that excavate the most suitable cavities for Hoopoes. In the short term, however, artificial cavities should be provided. To avoid the predation risks, including human disturbance, associated with tree nestboxes in the scarce foliage of modern orchards, secluded nesting sites could be erected in the numerous farm buildings. In addition, further research is also required on the distribution and ecology of the Hoopoe's favoured prey, namely Molecrickets.

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APPENDIX 1

Characteristics of the four breeding sites investigated using photography.

Site	Situation	Cavity location	Altitude (m)	Horizontal distance to the plain (m)	Year	Brood	Clutch size	No. of hatched eggs	No. of fledglings	Chick mortality (%)
A	Upper foothill	Tree	700	855	1989	1st	7	6	4	33
					1990	1st	8	7	4	43
					1990	2nd	5	4	4	0
B	Lower foothill	Concrete wall in vineyards	510	300	1990	1st	6	5	5	0
					1990	2nd	6	5	5	0
C	Plain	Nestbox	468	0	1990	2nd	6	5	5	0
D	Lower foothill	Stone wall	500	150	1990	1st	6	?	?	–

APPENDIX 2

Average dry body mass used for the estimation of the biomass of prey items provisioned to nestlings. Data from Arlettaz and Perrin (1995), Scarabaeidae larvae from A. Lugon.

		Dry body mass (g)			
		Mean	sd	Range	*n*
Annelida	*Lumbricus* sp.	0.38	0.17	0.14–0.68	15
Mollusca	*Arion ater*	0.23	0.16	0.06–0.51	8
Araneidae		0.05	0.03	0.01–0.12	49
Diplopoda	Iulidae	0.09	0.04	0.04–0.21	19
Orthoptera	*G. gryllotalpa*				
	Larvae, stage 2	0.09	0.01	0.07–0.10	4
	Larvae, stage 3	0.18	0.04	0.12–0.22	6
	Larvae, stage 4	0.36	0.01	0.35–0.37	3
	Larvae, stage 5	0.46	0.03	0.43–0.49	3
	Adult	0.68	0.04	0.62–0.71	4
	Gryllus campestris	0.22	0.06	0.15–0.40	17
	Acrididae (larvae)	0.04	0.02	0.02–0.08	13
Dictyoptera	*Mantis religiosa*	0.04	0.01	0.02–0.06	20
Heteroptera		0.02	0.01	0.01–0.04	18
Neuroptera	*Libelluloides* sp. (larvae)	0.03	–	–	1
Lepidoptera	Larvae	0.08	0.04	0.03–0.15	27
	Pupae	0.09	–	–	1
	Imagos	0.06	0.04	0.02–0.20	18
Diptera	Larvae	0.02	0.02	0.01–0.06	20
Hymenoptera	Formicidae	0.02	0.01	0.01–0.02	7
Coleoptera	Scarabaeidae (larvae)	0.09	0.02	0.06–0.14	11
	Other Coleoptera (larvae)	0.03	0.02	0.01–0.08	15
	Carabidae (imagos)	0.04	0.03	0.01–0.11	34
Reptilia	*Podarcis muralis*	0.56	0.22	0.28–0.91	8
	Eggs of *P. muralis*	0.21	–	–	1