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Seasonal and spatial variation of the Montagu's Harrier's *Circus pygargus* diet in Eastern Poland

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Capsule: The diet of the Montagu's Harrier *Circus pygargus* is variable and comprises the most available prey at a given time of the season. We found no evidence for a relationship between diet and land-use in the core foraging zone.
Aims: We investigated whether the diet of the Montagu's Harrier reflects the available prey and how it changes across the breeding season and in relation to land-use.
Methods: We analysed pellets collected at nests between 2007 and 2011. We looked for nonlinear patterns in the occurrence of prey categories in the pellets as a nonlinear function of the Julian date. Moreover, we tested whether the diet is affected by land-use within a radius of 2299 m from the nest.
Results: Four thousand four hundred and sixty-five prey items were found in 880 pellets and 76 prey remains collected at 63 sites. The diet did not depend on the land-use structure but showed a significant temporal variation.
Conclusions: The diet of the Montagu's Harrier follows the availability of the prey in the foraging habitat. We conclude that the type of land-use in the vicinity of the nesting habitat has a rather weak effect on the diet of the Montagu's Harrier.

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Predators hunt their preferred prey to maximize energy gain and minimize expenditures related to hunting and prey handling (Vezina 1985). Birds of prey selectively use habitats with the most profitable prey abundance-availability ratio, ensuring the highest hunting success and energy gain (Donazar *et al.* 1993, Zub *et al.* 2010). For instance, predators hunting in open landscapes usually prefer areas with short vegetation, which increases prey detectability and hunting success (Madders 2000, Mirski 2010), and therefore such areas are of great importance to the spatial distribution of predators. On the other hand, several species clearly change their diet when their main prey decreases in number, which in turn could strongly affect populations of the alternative prey (Redpath & Thirgood 1999, Reif *et al.* 2001, Zarybnicka *et al.* 2015). In birds of prey, high year-to-year variation in reproductive effort can be observed as a response to food availability (Arroyo *et al.* 2007), which can be especially well pronounced at higher latitudes when population cycles of microtine voles are observed (Therrien *et al.* 2014). On shorter time scales rapid behavioural reactions can be observed in response to sudden decreases in prey abundance or availability, for example, after heavy snowfall during winter. In such situations birds of prey drastically change their hunting behaviour and shift their diet towards alternative prey (Jędrzejewska & Jędrzejewski 1998).

In this study we investigated the spatial and temporal variation of diet composition in the largest population of the Montagu's Harrier *Circus pygargus* in Poland. The Montagu's Harrier's diet is much better studied in Western than in Eastern Europe, and new data should help verify whether there is a longitudinal gradient of diet diversity in this species (Terraube & Arroyo 2011). In addition, the agricultural intensification observed during recent years in Poland has affected the Polish farmland and the abundance of several species (Sanderson *et al.* 2013), and probably also the Montagu's Harrier. Landscape structure shapes foraging possibilities and may influence the diet of this species as it does in the Hen harrier *Circus cyaneus* (Amar *et al.* 2004). Finally, over recent decades the Montagu's Harrier appears to have changed its habitat from the previously preferred wetlands and grasslands to arable land. This shift was first observed in Western Europe (Ferrero 1995, Arroyo *et al.* 2002), and since the 1990s it has also been seen in Eastern Europe,

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including Poland (Jaszcz & Wójciak 1993, Krupiński *et al.* 2012). It most probably affects the foraging ecology of the species. Low genetic differentiation of the European population (Rutkowski *et al.* 2015) suggests that the habitat shift is driven by general ecological factors, not by a specialization of local populations.

Although over 30 studies have been conducted on the diet of Montagu's Harriers (reviewed in Terraube & Arroyo 2011), the effects of geographical location, change in agriculture and shift in the preferred habitat are only partly understood, mainly because diet variation has very rarely been investigated inter-seasonally and with large sample sizes. The first data on the diet of this species showed that birds and voles were most important in terms of biomass, and orthopterans were most important in terms of the frequency of prey taken (Mirski *et al.* 2009) but the data were collected only in one season and from a limited number of nests. In this paper, we hypothesize firstly that the Montagu's Harrier is a generalist raptor, so its diet in the extensive farmland of Eastern Poland will reflect the high diversity of prey categories (mammals, birds, lizards and invertebrates). Secondly, we expect that the seasonal variation of prey composition will correspond to availability. We predict that the number of consumed mammals (particularly voles) will increase during the breeding season as the numbers of the prey species increase (Ylönen *et al.* 1991, Borowski 2011). Birds are usually difficult to catch and hence raptors (e.g. Hen Harrier; Barnard *et al.* 1987, Redpath & Thirgood 1999) take mostly chicks and juveniles. We predict, therefore, that the percentage of birds in the diet of Montagu's Harriers should be highest around June, when juvenile birds are most abundant. We predict that orthopterans will be taken most frequently in July and August, when they reach adult sizes and are the most numerous (e.g. Jiguet 2002). Finally, we also hypothesize that the Montagu's Harrier's diet depends on the land-use type in the vicinity of the nest site (Amar *et al.* 2004), as land-use strongly affects composition of farmland birds (e.g. Berg *et al.* 2015) and other potential prey species.

Methods

Study area

The study was conducted in Eastern Poland, within approximately 40 km of Biała Podlaska city (52.03°N; 23.12°E). The study area was dominated by arable land (~70%) and grasslands (15%). In the arable land, potato and cereal were the most common types of crop, while grasslands consisted of meadows and pastures, located mostly in river valleys. The study region has a distinctive landscape structure, commonly consisting of small farms of an average size of 8 ha. This creates a mosaic of different crops and land-use types. The structure of the vegetation changes rapidly towards the end of May, when the first mowing starts (30 May on average), and again during crop harvesting (25 July on average).

Diet composition

The diet of the Montagu's Harrier was investigated using regurgitated pellets ($n = 880$) and prey remains ($n = 76$) collected either from nests (15% of samples) or from under nearby perches (85%). When nests lacked natural perches in close vicinity, a wooden pole was placed nearby to provide a perch to aid in the collection of pellets and prey remains. To avoid pseudo-replication, nests and perches within one breeding colony were treated as one sampling site in the spatial analysis. In total, pellets were collected from 63 separate sites (i.e. single nests or colonies). Fresh pellets were collected two to three times a month between May and September 2007–11. Each year, 12–24 (mean 18) sites were visited. From each site a mean of 25 pellets/prey remains were obtained through a season. A given site was followed for 1–3 years (mean 2.1 years).

Each complete pellet was treated as one sample. Prey remains and pellet fragments collected at a site on one visit were pooled to form one sample. Most of the prey items (~75%) were extracted from complete pellets. Pellets were disintegrated in order to extract all the solid material, for example, bones, beaks, scales and insect remains. Prey was determined using keys for the identification of mammals (Pucek 1984) and birds (Brown *et al.* 1987, Jenni & Winkler 1994). Mammals were identified by teeth and bones, birds by bones, beaks and feathers, and lizards by skulls, jaws, skin and scales. Insects were grouped into the three most frequent taxa. To avoid biases connected with secondary predation, remains of small beetles were omitted from the analysis when they were found together with lizard husks or bird remains in the same pellets. In some cases a bird feather expert was consulted (Aftyka S.). Prey was identified to species whenever possible, otherwise it was identified to the highest possible taxon (genus, order). Bone fragments and teeth found in different pellets were treated as separate prey. If prey was detected in one sample solely by fur, feathers or scales, it was assumed to belong to one individual. Biomass was calculated according to research from Eastern Poland (Jędrzejewska &

Jędrzejewski 1998). Grasshopper mass was estimated as 1.8 g using the mean mass of individuals caught in June 2011 ($n = 20$) in the study area. Coleopteran beetle mass was estimated as 1.0 g.

Land-use data

A radio-tracking study of breeding adult Montagu's Harriers (Krupiński D., unpubl. data) showed that, in the study area, a mean of 80% of fixes were within 2299 m of the nest. Habitat structure was, therefore, characterized within a radius of 2299 m from each nest site ($n = 63$ sites). We calculated coverage by land-use categories following the Corine Land Cover (CLC) 2006 using Geographic Information System (GIS) environment. As the majority of the categories were rare, we combined them into five main groups: (1) built-up areas, (2) arable land, (3) grasslands, (4) forests and (5) others. These groups were negatively correlated as they sum to one, so we combined them with the help of principle components analysis (PCA) into three orthogonal axes, which explained 92% of the variance of the five original variables (Table 1). The three axes were interpreted as land-use characteristics and included as independent variables in further modelling.

Table 1. Results of principal component analysis combining the five CLC land-use categories within 2299 m of harrier nests (or centres of colonies) into three orthogonal components (PC1-3) used in further modelling. Loadings below 0.4 are not shown.

Original variables	PC1	PC2	PC3
Arable land	−0.94		
Grassland	0.75		−0.58
Built-up areas	0.56	0.68	
Other		−0.94	
Forests			0.97
% cumulative variance	36	65	92

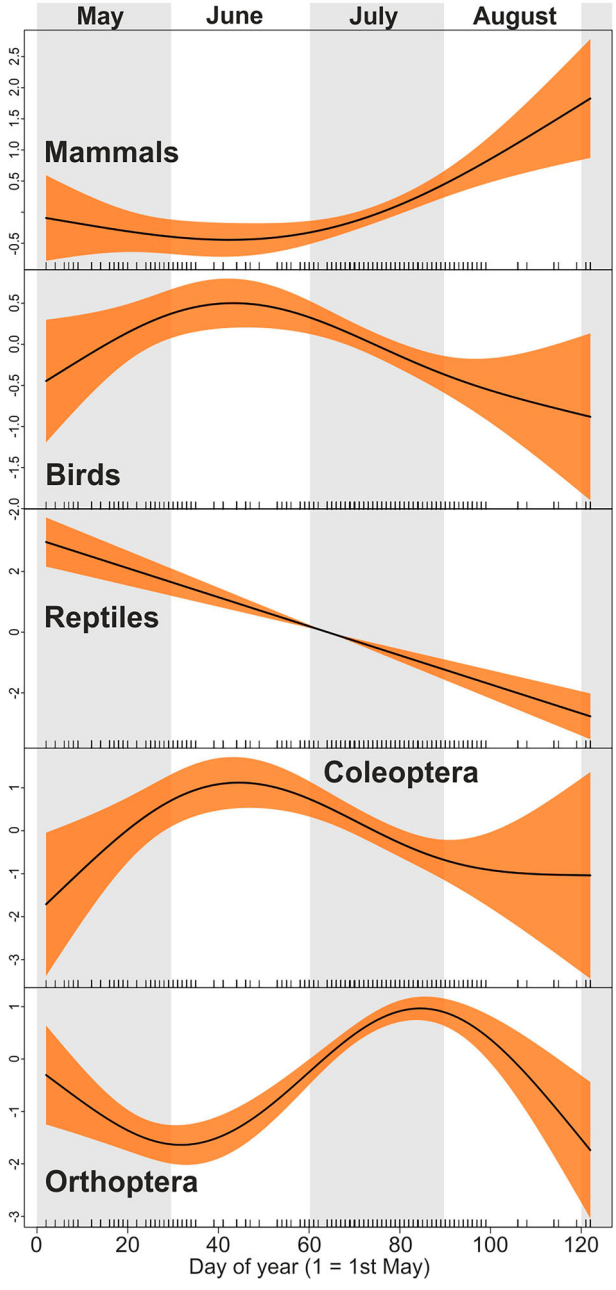

Figure 1. Variability of occurrence of the five main prey categories in the 880 fresh pellets of the Montagu's Harrier collected in the breeding seasons of 2007–2011 in an agricultural landscape of Eastern Poland. The fits are based on models presented in Table 3, *y*-axes present residual values.

Statistical analysis

We analysed the temporal and land-use-driven variation in the diet of the Montagu's Harrier by testing whether the frequency of the five main prey categories (mammals, birds, reptiles, orthopterans and carabid beetles) in 880 fresh pellets of known collection date varied with time during the breeding season and land-use in the vicinity of pellet collection site. For this purpose we used generalized additive mixed models (GAMM) with a binomial error distribution and logit link, implemented in R (R Development Team 2015) with the *mgcv* package (Wood 2006). We used presence-absence of each prey category in each pellet as a separate response variable (separate GAMMs were performed for each prey category, five in total). The day of the year, starting from the first month of data collection (1 = 1 May), was used as a continuous explanatory variable and fitted with a cubic regression spline, as we expected a nonlinear relationship between the date and the occurrence of a particular prey type in the diet. This method enabled us to fit nonlinear functions linking the dependent and independent variables, with the degree of smoothness optimized by

generalized cross-validation (Wood 2006). The three land-use components (PC1-3) were included as continuous variables, while site (i.e. location where the pellets were found) and year were treated as random factors.

Results

Overall, we identified 4465 prey items of total weight reaching almost 30 kg. The Montagu's Harrier most frequently fed on invertebrates, of which large-bodied orthopterans predominated by abundance (Table 2). We recorded over 3000 bush-crickets *Tettigonia* and nearly 400 crickets Gryllidae. However, although numerous, they constituted a relatively small proportion of the overall consumed biomass (20.2%). In respect to biomass, the primary prey were birds (41.6%) followed by mammals (33.3%). Bird prey were mainly small and medium-sized farmland species: Skylark *Alauda arvensis*, Yellow Wagtail *Motacilla flava*, Meadow Pipit *Anthus pratensis* and Whinchat *Saxicola rubetra*. Among the identified mammal prey items, the Common Vole *Microtus arvalis* was the most numerous. Lizards appeared more frequently in the diet than did amphibians.

The diet composition of the Montagu's Harrier was not constant over the breeding season and we found strong nonlinear patterns. The probability of the occurrence of mammals in the diet was low at the beginning of the breeding season but increased rapidly in the second half of the breeding season. The odds of finding a mammal in pellets were over sevenfold higher at the end of August as compared to May. The reverse of this pattern was found for birds; their occurrence in the diet increased from the beginning of May until mid-June and markedly decreased afterwards. Although reptiles were scarce in the diet, their occurrence was highest at the very beginning of the breeding season and decreased linearly thereafter. Carabid beetles were most common in the diet in June while the occurrence of Orthoptera increased from the end of May, with a peak around the end of July (Figure 1, Table 3).

Table 2. Diet composition of the Montagu's Harrier in Eastern Poland in 2007–2011.

Prey category	Number	Percentage of number	Individual biomass (g)	Total biomass (g)	Percentage of biomass
Microtus unident	208	4.7	20.1	4178.7	14.0
Microtus arvalis	105	2.4	19.0	1995.0	6.7
Microtus oeconomus	19	0.4	26.0	494.0	1.7
Arvicola terrestis	1	0.0	130.0	130.0	0.4
Apodemus spp.	15	0.3	17.0	255.0	0.9
Apodemus agrarius	8	0.2	17.0	136.0	0.5
Rodentia unident.	26	0.6	20.2	525.2	1.8
Talpa europaea	3	0.1	95.0	285.0	1.0
Sorex spp.	2	0.0	8.0	16.0	0.1
Small mammals unident.	55	1.2	20.8	1142.9	3.8
Medium mammals unident.	3	0.1	200.0	600.0	2.0
Lepus sp.	1	0.0	200.0	200.0	0.7
Mammals Σ	446	10.0		9957.8	33.3
Alauda arvensis	57	1.3	37.0	2109.0	7.0
Anthus spp.	13	0.3	19.0	247.0	0.8
Motacilla flava	15	0.3	17.0	255.0	0.9
Saxicola rubetra	3	0.1	18.0	54.0	0.2
Fringilla coelebs	2	0.0	25.0	50.0	0.2
Emberiza citrinella	1	0.0	30.0	30.0	0.1
Miliaria calandra	2	0.0	35.0	70.0	0.2
Delichon urbicum	1	0.0	19.0	19.0	0.1
Phasianus colchicus	1	0.0	1250.0	1250.0	4.2
Phylloscopus spp.	1	0.0	9.0	9.0	0.0
Carduelis cannabina	1	0.0	18.0	18.0	0.1
Turdus spp.	1	0.0	70.0	70.0	0.2
Turdus philomelos	1	0.0	70.0	70.0	0.2
Coturnix coturnix	1	0.0	110.0	110.0	0.4
Corvideae spp.	1	0.0	170.0	170.0	0.6
Eggs	24	0.5	9.0	216.0	0.7
Small birds unident.	160	3.6	41.7	6668.8	22.3
Medium birds unident.	10	0.2	105.0	1050.0	3.5
Birds Σ	295	6.6		12 465.8	41.6
Lacerta spp.	105	2.4	12.0	1260.0	4.3
Rana spp.	1	0.0	13.5	13.5	0.0
Amphibians and reptiles Σ	106	2.4		1273.5	4.3
Coleoptera spp.	166	3.7	1.0	166.0	0.6
Tettigonia spp.	3053	68.4	1.8	5373.3	17.9
Gryllus spp.	399	8.9	1.8	702.2	2.3
Invertebrates Σ	3618	81.0		6241.5	20.8
Total	4465			29 938.6	

Table 3. Summary of the five GAMM explaining occurrence of the five main prey categories in 880 pellets of the Montagu's Harrier collected in Eastern Poland in 2007–2011. In the models three PCA components describing land-use are included (see Table 1) and day of year is fitted with spline. For the latter, estimated degrees of freedom (edf) are given, $P < 0.05$ are marked in bold.

	Mammals		Birds		Reptiles		Coleoptera		Orthoptera	
Predictor	*B* (se)	*P*	*B* (se)	*P*	*B* (se)	*P*	*B* (se)	*P*	*B* (se)	*P*
Intercept	−0.04 (0.11)	0.736	−0.79 (0.12)	**<0.001**	−3.07 (0.23)	**<0.001**	−2.88 (0.27)	**<0.001**	−0.57 (0.14)	**<0.001**
PC1	−0.17 (0.10)	0.111	0.07 (0.11)	0.491	−0.14 (0.23)	0.549	0.43 (0.24)	0.070	0.00 (0.11)	0.984
PC2	0.04 (0.11)	0.725	0.08 (0.11)	0.492	−0.28 (0.19)	0.132	−0.27 (0.25)	0.272	−0.12 (0.12)	0.334
PC3	0.01 (0.11)	0.932	−0.11 (0.11)	0.327	0.06 (0.16)	0.717	−0.23 (0.24)	0.328	0.03 (0.12)	0.797
s(day)	edf = 2.29	**<0.001**	edf = 2.48	**0.025**	edf = 1.00	**<0.001**	edf = 2.66	**0.021**	edf = 2.93	**<0.001**

The diet composition of the Montagu's Harrier was not significantly affected by the three land-use variables (PC1-3, $P > 0.07$ in all cases; Table 3).

Discussion

The list of prey species and the quantity of individual prey types in the overall biomass consumed confirmed our predictions and showed a high diversity in the diet of the Montagu's Harrier in Eastern Poland. The species is considered to be a generalist, hunting the most available prey, which varies seasonally (Arroyo 1997) and geographically (Terraube & Arroyo 2011). In our study the harriers hunted mainly birds in terms of biomass, including some heavy species such as the Common Pheasant *Phasianus colchicus* (see also Redpath & Thirgood 1999), and orthopterans in terms of number, as found in most other studies (Terraube & Arroyo 2011).

The high diversity of the diet in this generalist raptor is likely to be driven by the generally high biodiversity of potential prey within the Polish agricultural landscape. This is also suggested by the percentage of orthopterans, which was higher than that reported in most other studies (Terraube & Arroyo 2011). The study area is dominated by extensively managed farmland and patches of a given land-use type are usually small, used over variable time periods and with diverse vegetation height, which results in a complex mosaic. This in turn promotes diversity of birds, mammals and invertebrates.

In several studies on the diet of the Montagu's Harrier, the percentage of microtine voles was higher compared to our results, especially in the case of prey brought to nestlings (Maurel & Poustomis 2001, Koks *et al.* 2007). This difference most plausibly stems from the abundance of voles relative to alternative prey in the foraging habitat. However, Koks *et al.* (2007) suggested that the frequency of voles in the diet increased with agricultural intensification. It seems that agricultural intensity in the Netherlands, where Koks *et al.* (2007) studied Montagu's Harriers, was higher than in Eastern Poland. This supports the hypothesis that the abundance of voles in the diet reflects environmental conditions, since the lower densities and species richness of some common farmland birds in western parts of Europe may force Montagu's Harriers to feed predominantly on voles. Still, it cannot be excluded that our data are biased towards some prey categories as they are based on material (pellets, remains) found in or near nests. Redpath *et al.* (2001) showed that in the Hen Harrier, analysis of diet using pellets overestimated mammals and underestimated birds in the diet, but were a good indicator of prey diversity. Also, in the Marsh Harrier *Circus aeruginosus* pellets were found to overestimate mammals in contrast to direct observations, but at the same time reflected the diet diversity no better than direct observations combined with a study of prey remains (Brzeziński & Żmihorski 2009).

High diet diversity could reflect high biodiversity within the habitat of a generalist predator or poor availability of favourable prey in a specialist predator. The Montagu's Harrier sometimes specializes on one kind of prey, such as lagomorphs in Central Spain. Arroyo & Garcia (2006) found that diet diversity was negatively correlated with proportion of hares *Lepus* in diet. Moreover, years with higher diet diversity were associated with a higher rate of nest failure. In our study site, however, there was no abundant prey of similar body size so we would expect the Montagu's Harriers to act as generalist predators and for their diet to reflect the wide diversity of potential prey within the farmland of Eastern Poland. Results obtained by us are in accordance with the findings of Terraube & Arroyo (2011), who showed that the diet of the Montagu's Harrier is more varied at lower latitudes and probably also at higher longitudes. Also, the high proportion of diet biomass taken up by birds is a common finding of similar studies from elsewhere in Europe (Terraube & Arroyo 2011).

Effect of seasonal variability

The observed patterns of temporal variation of the main prey categories in the diet of the Montagu's Harrier seem

to follow the availability of prey in the habitat, as predicted in the hypothesis. Throughout the breeding season, small mammals, especially rodents, markedly change their abundance. The lowest numbers are recorded in spring and the highest numbers are observed at the end of summer. This pattern of rodent abundance is an important factor underlying the diet composition of many birds of prey in temperate Europe (Jędrzejewska & Jędrzejewski 1998). This is consistent with the concept that the diet dynamics of the Montagu's Harrier corresponds to the expected dynamics of vole availability. Surprisingly, in Central Spain the opposite pattern was observed; as the season progressed the percentage of small mammals decreased in the diet of Montagu's Harriers (Arroyo 1997). The occurrence of birds in the diet was highest in June, when the abundance of fledglings and young individuals, which are relatively easy to catch for predators, is the highest. In July and August the frequency of birds gradually decreased, which may have been caused by increasing availability of rodents. Orthopterans most densely inhabit grasslands and ecotones, and their importance in the diet most probably results from their higher availability during summer. Also at that time they probably act as training-prey for recently fledged Montagu's Harriers (Kitowski 2005). Contrary to our predictions, we recorded a linear decrease with season in the occurrence of reptiles in the diet; perhaps the availability of other prey types is crucial, and the dynamics of lizards in the diet mainly reflects the availability of mammals, birds and orthopterans. The high occurrence of reptiles in early spring may be caused by low availability of mammals (because their densities are still low) and birds (no fledglings yet available). This suggests that reptiles, mainly lizards, could act as alternative prey, which are used by the Montagu's Harrier when other prey types are less available.

Lack of effect of land-use

We did not find any effect of land-use type on diet composition in the Montagu's Harrier, as predicted by our hypothesis, although such habitat–prey relationships have been detected for other harrier species (Amar *et al.* 2004). This may be explained by several factors. First, our former studies concerning habitat use, based on radio tracking (Krupiński, pers. data), showed that the Montagu's Harrier forages over a very large area (up to 26 km from the nest, Krupiński, pers. data). We selected the radius of 2299 m to cover most (80%) of the foraging activity of the Montagu's Harrier. However, some important hunting areas could be located outside this threshold distance. Secondly, the mosaic of different land-use types in the study area that causes the link between diet composition and land-use structure is difficult to investigate. Finally, the lack of effect of land-use may also result from the fact that the resolution (patches of 25 ha or bigger) of the CLC data may not sufficient for the purpose of this study: small patches of habitat preferred by the Montagu's Harrier could be undetected in the CLC.

Nevertheless, other authors found some general links between diet and habitat in the Montagu's Harrier. Corbacho *et al.* (2005) observed that its diet was more diverse in pasture land, where it also hunted larger prey. Terraube & Arroyo (2011) reported that insects were more often hunted in cereal-pasture habitats, while small birds and reptiles were hunted in cereal-dominated landscapes.

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