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Diet of the Black-eared Wheatear *Oenanthe hispanica* in relation to food availability in two arid shrubsteppes

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Abstract - The diet of Black-eared Wheatear *Oenanthe hispanica* was studied by faecal analysis in two arid shrubsteppe zones of southeast Spain. A total of 197 faeces collected in spring and summer contained recognizable remains of 826 prey. Formicidae, Coleoptera and Orthoptera were the main prey taxa in the diet, both in number of prey items as well as in the amount of biomass provided. Diet composition showed marked variations throughout the study period; differences between zones were also found. Prey size was smallest in mid-summer, when the main prey type was predominantly worker ants, and largest in spring and late summer. Prey availability, measured using pitfall traps, was related to diet. Only Orthoptera and Heteroptera were positively selected over the entire study period. Ants, due to their great abundance, appeared to be consumed below availability, despite their high frequency of consumption. The vegetal fraction in the diet was small, consisting mainly of Caper (*Capparis spinosa*) fruit. The Black-eared Wheatear appears to behave as a generalist feeder, with a diet based on the abundant ants and supplemented with other more profitable groups when found.

Introduction

Dietary strategies of birds inhabiting arid zones (habitats characterised by low productivity), may be critical for their survival (Louw and Seely 1982, Wiens 1991). This aspect of bird's biology is relatively well known in most part of northern and central European passerines, though far from complete. However, ignorance in this regard is especially noteworthy in those species inhabiting open, non-forested areas, mainly because the difficulty of capturing and managing specimens in usually low-density populations. In addition, while most northern species of birds have been studied for decades, many birds of the Mediterranean Basin have received only cursory attention.

Only during recent years there is an increasing interest in these habitats and their inhabiting birds (see e.g. Sanz and Fernández 1996). Nonetheless, we know very little about the diet of species such as the Black-eared Wheatear *Oenanthe hispanica*, that are distributed in deforested lands, dry grassland pastures and rocky zones of the Mediterranean Basin. Spain is one of the countries in which the species is most widely distributed (Cramp 1988) and, as with most Iberian steppe passerines, their basic life-history traits are almost unknown. Some aspects of its biology, such as reproductive success (Suárez and Manrique 1992) and foraging behaviour (Santos and Suárez 1985) have been analysed but its diet poorly studied. Despite this lack of information, only six stomachs analysed by Gil-Lletget (1945) and a nestling-diet study performed by Suárez (1987) provide dietary data for this species in the Iberian Peninsula. Even for their entire distribution area, previous investigation is restricted to Lostok (1982) in the former USSR, and Cornwallis (cited in Cramp 1988) in Iran.

The aim of this work is to describe diet of the Black-eared Wheatear in southern Spain during the breeding and postbreeding period (April-September, the usual period of residence of this migratory species in Spain), analysing the monthly variations in diet as well as the diet in relation to food availability.

Study area and methods

The general study area is the Guadix-Baza Basin, a Neogene basin surrounded by high mountains (1700-3000 m a.s.l.), at an altitude 700-1100 m a.s.l. The climate is continental Mediterranean, with warm (average temperature 25.0°C in July) and dry summers (Castillo-Requena 1989). During the year of study, 1991, rainfall was 281 mm in Baza and 263 mm in Guadix. Field work was carried out in two seasonal watercourses, (called "ramblas"), which remain dry

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most of the year. The two study sites were the Barranco del Espartal (30sWG2754, TM Baza, 750 m a.s.l.; hereafter Baza), a rambla in a badland landscape with a substrate of silt with gypsum sediments, and the Rambla del Grao (30sVG8735, TM Guadix, 950 m a.s.l.; hereafter Grao), a rambla with clay soil. The vegetation is sparse in both areas (33% shrub cover in Baza, 17% in Grao), mainly shrubs of *Salsola* spp., *Artemisia* spp. and *Retama sphaerocarpa*, and scant grasses and forbs. Bare ground reaches 46% cover in Baza and 60% in Grao. Further details about the study areas can be found in Hódar (1996).

Diet analyses were based exclusively on faecal samples, collected between April and September 1991. Although faecal analysis may produce biases in estimating the importance of some prey groups, because of differences in their digestibility (Jenni *et al.* 1992), it appears to provide accurate information for insectivorous birds (Ralph *et al.* 1985, Rosenberg and Cooper 1990). Faeces were collected every two weeks, surveying the usual hunting perches of birds. Most of perches was marked and bird visits noted, in order to avoid confusions with Black Wheatear *Oenanthe leucura* and Great Grey Shrike *Lanius excubitor*, also present in the zones and with similar perching behaviours. I spent from 10 to 17 days per month to record avian foraging and perches use, so that collections were made only from perches exclusively used by Black-eared Wheatear. The ground close to the perch and the perch itself were cleaned after each visit. Only complete faeces were collected; those damaged, broken or deteriorated were discarded.

The number of birds sampled roughly corresponds to five pairs, in both sites, although I made no attempt in order to exactly delimitate territories. To equally distribute the sampling effort between pairs, sampling perches were distributed as evenly as possible in the study area, and the number of excrements per perch and month was limited to up to five. Since sampling was always made on the same area and all excrements were collected, I assume that every bird living in the area had the same probability to be sampled. I also took advantage of active birds targeted at the moment of defecating. I chose these non-aggresive methods of sampling, despite their inconveniences and difficulties, because Black-eared Wheatear is strictly protected under Spanish laws, it is difficult to capture by usual live-trapping methods (as mist-nets), and shows low densities in the study area (0.4-1.2 birds/10 Ha, Hódar 1996).

Faeces were dispersed in water and examined under a 10-40x binocular microscope equipped with a micrometer. Prey remains were identified, sorted and measured. Prey were usually determined to the lowest taxonomic level possible. Measurements of characteristic prey pieces remaining in faeces allowed an estimate of the prey's body size and biomass, by means of a series of regression equations previously developed (Hódar 1997). When this estimation was not possible, biomass was inferred as the mean of the corresponding taxonomic group for that month and zone.

Prey availability was estimated in Baza by means of 36 pitfall traps (6.4 cm in diameter) scattered throughout all available microhabitats in the rambla, placed biweekly (sampling period 48 h) during the six months of study, in order to assess the diet selectivity by Black-eared Wheatear. Pitfalls were chosen for ground-dwelling arthropods (see e.g. Cooper and Whitmore 1990) because at both sites Black-eared Wheatear captures most of its prey on the ground (Santos and Suárez 1985, Hódar 1993). Pitfall traps are usually considered a biased estimator of availability, being strongly dependent on the mobility pattern of arthropods; however, several studies expand upon these opinions (e.g. Cooper and Whitmore 1990, Andersen 1991). Caution is needed in interpreting from pitfall traps results, because of the limitations involved, and, certainly, no method of trapping insects gives an accurate idea about how the bird perceives availability. In view of the above reported, capture data in pitfalls were modified for a better adjustment with diet data (Hutto 1990, Wolda 1990). Firstly, I removed Acarina, Collembola and all arthropods with body size <2 mm from pitfalls, because these groups of very small size were not eaten by wheatears (Wolda 1990). Secondly, I arbitrarily assigned a frequency of 0.01% to the prey types that appeared in diet but not in the pitfalls. Because birds cannot prey upon groups that are not present, this was required for calculations of selectivity. This correction was applied to 9 out of 70 cases. Selectivity was measured by means of Jacobs' S selectivity index (Jacobs 1974), $S = O_i - A_i / O_i + A_i - 2O_iA_i$, being Ai the proportion in which a resource item is available and Oi the proportion in which this resource is used (both Ai and Oi expressed between 0 and 1; e.g. O_i=%F/100).

Diet data were computed on a monthly basis, both percentage of occurrence (percentage of faeces in which an item appeared), numeric frequency (percentage of items belonging to a prey class with respect to the total of prey items) and estimated biomass (percentage of biomass belonging to a prey class with respect to the total biomass of all prey items; Rosenberg and Cooper 1990). For vegetal material, only percentage of occurrence was calculated. Comparisons of diet compositions were made with G tests, whereas prey sizes were compared with the Mann-Whitney and Kruskal-Wallis tests. Non-parametric tests were applied because of the heteroscedasticity and non-normal distribution of prey sizes (Zar 1996).

Results

A total of 197 faeces (142 in Baza, 55 in Grao) were collected during the sampling period. In Grao, collections were not possible between June and July, because breeding Wheatears were widely dispersed in the hilly surroundings of the rambla, and it was not possible to locate reliable perches. Subsequent analysis of the faeces gave 826 prey items (587 in Baza, 239 in Grao).

Tables 1 and 2 show the diet data for Black-eared Wheatear in Baza and Grao, respectively. As a whole, the diet differed significantly between zones, both in taxonomic composition (G=44.73, df=12, $p<0.001$, G test) and in prey size (Z=4.40, $p<0.0001$, Mann-Whitney test). In both zones, the main groups consumed were Formicidae, Coleoptera and Orthoptera, according to frequency, but this rank was reversed when considering biomass.

Through monthly sequences, pronounced changes in diet composition were found. In Baza, Scarabaeidae beetles were the main prey for the birds newly arrived in April, because these beetles emerged in this month and were conspicuous and easy to capture. From May onwards, diet was based on ants, mainly *Messor* sp. and *Camponotus* sp., but complemented with Heteroptera and, increasingly during summer, grasshoppers. During breeding, in May and June, spiders and even a small lizard were caught. In August and September, grasshoppers and ants were the main components of the diet, although sometimes birds fed on Caper *Capparis spinosa* fruits, which ripen at this time and are especially abundant in Baza. In Grao, the pattern was similar, but Scarabaeidae are not present; therefore, diet was based on ants in April and May. In August, predation on Orthoptera seemed to have been even heavier than in Baza, but the small sample size prevents a defini-

Table 1. Taxonomic composition of the diet of the Black-eared Wheatear in Baza. Data are reported as percentage of occurrence (%P), numeric frequency (%F) and biomass (%B). Prey length is expressed in mm.

	April			May			June			July			August			September		
Group	%P	%F	%B	%P	%F	%B	%P	%F	%B	%P	%F	%B	%P	%F	%B	%P	%F	%B
Arachnida	0	0	0	6.2	2.4	1.1	0	0	0	0	0	0	0	0	0	19.0	6.5	3.8
Araneae	25.0	6.7	13.7	15.6	5.9	20.6	7.7	1.9	10.3	10.0	1.9	7.7	8.0	1.5	6.4	9.5	2.6	9.0
Isopoda	0	0	0	6.2	2.4	0.6	15.4	3.7	1.5	0	0	0	0	0	0	0	0	0
Myriapoda	25.0	6.7	13.2	3.1	1.2	4.0	3.8	0.9	0.1	0	0	0	0	0	0	4.8	1.3	4.3
Orthoptera	25.0	6.7	5.8	15.6	8.2	24.7	30.8	10.3	33.0	43.3	9.0	38.7	48.0	9.8	55.4	47.6	15.6	60.1
Homoptera	12.5	3.3	0.1	9.4	3.5	0.1	3.8	0.9	0.1	0	0	0	24.0	0.8	0.1	0	0	0
Heteroptera	62.5	20.0	14.5	18.8	7.1	7.3	15.4	3.7	5.7	20.0	3.9	3.5	12.0	3.0	3.9	19.0	5.2	3.9
Lepidoptera Larvae	0	0	0	6.2	2.4	1.1	3.8	1.9	2.7	23.3	4.5	2.3	32.0	2.3	0.1	4.8	1.3	0.6
Coleoptera	100	50.0	52.5	84.4	11.8	10.5	38.5	10.3	15.0	66.7	20.0	36.8	60.0	13.5	9.8	76.2	22.1	11.6
Carabidae	0	0	0	6.2	2.4	0.1	7.7	1.9	0.1	0	0	0	4.0	1.5	0.1	0	0	0
Tenebrionidae	25.0	6.7	7.9	9.4	3.5	7.0	7.7	1.9	6.3	30.0	7.7	28.4	8.0	1.5	3.9	9.5	2.6	5.5
Scarabaeidae	75.0	30.0	38.7	9.4	3.5	3.3	0	0	0	0	0	0	0	0	0	4.8	2.6	2.0
Curculionidae	0	0	0	0	0	0	0	0	0	6.7	1.3	0.2	8.0	1.5	0.5	28.6	7.8	1.1
Coleopt. others	50.0	13.3	5.9	6.2	2.4	0.1	23.1	6.5	8.6	46.7	11.0	8.2	40.0	9.0	5.3	33.3	9.1	3.0
Hymenoptera	12.5	3.3	0.1	59.4	41.2	15.0	96.2	62.6	30.6	76.7	60.6	10.9	88.0	68.5	24.3	61.9	45.5	6.7
no Formicidae	0	0	0	28.1	10.6	6.5	34.6	8.4	8.7	23.3	4.5	1.1	56.0	5.3	0.2	0	0	0
Formicidae	12.5	3.3	0.1	37.5	30.6	8.5	80.8	54.2	21.9	73.3	56.1	9.8	88.0	63.2	24.1	61.9	45.5	6.7
Insecta others	12.5	3.3	0.3	31.2	12.9	2.3	11.5	3.7	1.3	0	0	0	4.0	0.8	0.1	0	0	0
Lacertidae	0	0	0	3.1	1.2	12.9	0	0	0	0	0	0	0	0	0	0	0	0
Capparis fruit	0	–	–	0	–	–	0	–	–	0	–	–	8.0	–	–	14.3	–	–
Vegetal others	0	–	–	9.4	–	–	0	–	–	0	–	–	4.0	–	–	0	–	–
Number of samples		8			32			26			30			25			21	
Prey identified		30			85			107			155			133			77	
Prey measured		15			41			57			100			96			56	
Prey length, $\overline{X}$±SD		10.21±2.42			8.95±5.39			7.68±3.94			5.41±3.60			6.83±5.41			8.54±7.47	

Table 2. Taxonomic composition of the diet of the Black-eared Wheatear in Grao. Data expressed as in Table 1.

Group	April %P	April %F	April %B	May %P	May %F	May %B	August %P	August %F	August %B
Arachnida	0	0	0	30.0	8.9	14.8	0	0	0
Araneae	16.7	6.6	25.4	20.0	4.4	14.5	0	0	0
Myriapoda	0	0	0	10.0	2.2	14.4	14.3	6.7	2.1
Orthoptera	22.2	5.5	6.1	70.0	21.5	36.1	85.7	53.3	82.1
Heteroptera	5.6	1.1	0.3	20.0	4.4	3.8	28.6	13.3	10.4
Lepidoptera Larvae	11.1	2.2	10.7	16.7	5.2	5.3	0	0	0
Coleoptera	55.6	18.7	44.9	63.3	16.3	7.4	28.6	20.0	5.2
Carabidae	0	0	0	3.3	0.7	0.1	0	0	0
Tenebrionidae	33.3	9.9	39.0	0	0	0	0	0	0
Curculionidae	5.6	1.1	0.2	13.3	3.0	0.3	0	0	0
Coleoptera others	38.9	7.7	5.7	46.7	12.6	7.0	28.6	20.0	5.2
Hymenoptera	50.0	62.6	11.2	30.0	37.0	3.9	14.3	6.7	0.2
no Formicidae	16.7	3.3	5.0	3.3	0.7	0.9	0	0	0
Formicidae	44.4	59.3	6.2	30.0	36.3	3.0	14.3	6.7	0.2
Insecta others	16.7	3.3	1.3	0	0	0	0	0	0
Vegetaltems	5.6	–	–	0	–	–	0	–	–
N° samples		18			30			7	
Prey identified		89			135			15	
Prey measured		74			107			10	
Prey length, $\overline{X}$±SD		7.67±4.46			9.06±5.57			17.15±7.49	

Table 3. Availability (Av., monthly percentage of captures in pitfalls) and selectivity values (S, Jacobs' S index) for the different prey types found in the diet of the Black-eared Wheatear in Baza.

Group	April Av.	April S	May Av.	May S	June Av.	June S	July Av.	July S	August Av.	August S	September Av.	September S
Arachnida	0	—	0.31	0.78	0.43	-1.00	0.22	-1.00	0.26	-1.00	0.01	1.00
Araneae	6.25	0.03	4.76	0.12	4.28	-0.40	2.23	-0.07	0.26	0.71	2.28	0.07
Isopoda	0.69	-1.00	2.00	0.09	1.88	0.34	1.45	-1.00	1.02	-1.00	2.28	-1.00
Myriapoda	0.01	1.00	0.01	0.98	0.26	0.57	0	–	0	–	0.01	0.98
Orthoptera	2.43	0.48	2.30	0.59	1.11	0.82	1.23	0.78	0.51	0.91	0.91	0.91
Homoptera	13.19	-0.63	7.83	-0.39	2.65	-0.49	2.34	-1.00	0.13	0.71	2.05	-1.00
Heteroptera	1.04	0.92	0.61	0.85	0.51	0.77	0.22	0.89	0.06	0.96	0.46	0.85
Lepidopt. larvae	1.04	-1.00	1.08	0.38	0.09	0.91	0.01	1.00	0.01	0.99	0.01	0.98
Carabidae	0.35	-1.00	0.46	0.68	0.09	0.91	0.33	-1.00	0.01	0.99	0.23	-1.00
Tenebrionidae	18.06	-0.51	7.07	-0.34	2.57	-0.16	4.91	0.24	1.28	0.08	4.78	-0.31
Scarabaeidae	2.08	0.91	0.46	0.78	0.94	-1.00	0	–	0.06	-1.00	0.23	0.84
Curculionidae	3.82	-1.00	0.77	-1.00	0.09	-1.00	0.01	0.98	0.13	0.85	1.82	0.64
Coleopt. others	5.90	0.42	7.99	-0.56	2.05	0.54	1.79	0.74	0.51	0.90	5.69	0.25
Hymenoptera	1.74	-1.00	2.76	0.62	1.71	0.68	1.90	0.42	0.70	0.77	1.14	-1.00
Formicidae	34.38	-0.88	49.31	-0.37	78.44	-0.51	82.25	-0.57	94.43	-0.82	76.54	-0.59
Insecta others	9.03	-0.48	12.29	0.04	2.91	0.13	1.12	-1.00	0.64	0.08	1.59	-1.00

tive conclusion. These shifts reflect variations in prey size, which was strongly influenced by the amounts of ants consumed. In Baza, prey size was smallest in mid summer (Table 1), the period of maximum ant predation, and increased at the beginning and end of study period, when large prey such as Scarabaeidae and Orthoptera were consumed. Overall differences in size throughout study period were significant ($H=53.96$, $df=5$, $p<0.0001$, Kruskal-Wallis test).

Selectivity was negative for most groups, even for heavily consumed groups as ants (Table 3). Orthoptera and Heteroptera showed a consistent positive selection throughout the study period, whereas Lepidoptera larvae and Curculionidae became progressively more selected with the advance of the summer. In fact, their consumption was almost uniform, but availability progressively diminished. Most of the other groups, usually very scantily available and only occasionally captured by the Black-eared Wheatear, changed from selection to rejection and viceversa without a clear pattern.

Discussion

The diet recorded for Black-eared Wheatear in Guadix-Baza area agrees with previous studies on the species. Lostok (1983) reported the same main groups in the SW of the former USSR during the breeding period, although in the present study ants were slightly less important and caterpillars more. Cornwallis (cited in Cramp 1988) recorded the same groups in Iran, and only a higher consumption of fruit in September contrasts notably with the present data. In Spain, the only preceding dietary data on the adult Black-eared Wheatear, from six stomachs analysed by Gil-Lletget (1945), are consistent with the present study in terms of the main prey found.

Little variation was evident in the main dietary groups between zones, although overall taxonomic composition showed significant differences. The number of groups consumed reached its maximun in May and June, the beginning of breeding period, due to the necessity of searching for less sclerotised and hence more profitable prey (cf. Karasov 1990) to feed to nestlings (see also Royama 1976, Peris 1980, Suárez 1987). In fact, there is a noteworthy difference between the main dietary groups for adults and nestlings. Suárez (1987) recorded Lepidoptera (both larvae and adults), Orthoptera, Coleoptera and Diptera as staple food for Black-eared Wheatear nestlings in central Spain, while for adults in Baza only Orthoptera and Coleoptera attained a certain degree of importance (especially in terms of biomass). After the fledging stage, the bird's diet is based on ants, grasshoppers and darkling beetles. Orthoptera, though difficult to capture because of its jumping and flying ability, are abundant and diurnal, and a prey representing a substantial benefit in biomass.

The only group of dietary importance with positive selectivity was that of grasshoppers. Some scarce groups showed positive dietary selectivity, such as caterpillars, because of low frequency in pitfall traps. This was not due to sampling bias: a parallel study on the arthropods living in the vegetation (Sánchez-Piñero 1994) showed that caterpillars were in fact very infrequent in shrubbery during mid- and late summer; their absence in pitfalls was due to a true scarcity in the study area, although caterpillars may also be used preferentially for feeding young (see above). Several other groups showed incidentally positive selectivity as a consequence of peaks in availability, such as scarabeid beetles in spring and soil weevils in late summer.

The presence of ants in the diet of birds is usually considered due to a scarcity of optimal resources (Herrera 1983). Ants are small, highly sclerotized, and sometimes have formic acid as a defence. In woody zones of southern Spain, insectivorous birds eat ants mainly during winter, shifting to more profitable prey when available (Herrera 1978, 1983). However, it has been suggested (Soler *et al.* 1991) that some ant species, as *Messor* spp., may be profitable to birds due to conspicuous behaviour and low investment of formic acid. Ants represent around 60% of total insect captures in pitfall traps, and high abundance in pitfalls, despite dietary importance, indicated rejection (Table 3); that is, ant consumption is lower than availability. Taking into account this rejection of ants, it seems that Black-eared Wheatear seeks profitable prey, but accepts ants when no other prey is available. Similar conclusions were drawn for the Black Wheatear, studied in the same zones (Hódar 1995). Due to the abundance and predictability of ants, because of the fixed location of nests and aggregated foraging pattern, and the low availability or difficult capture of other groups (grasshoppers), ants reach strong prominence in the diet despite their assignment as alternative food (Herrera 1983).

Fleshy fruits are seldom consumed, despite that the Black-eared Wheatear is able to consume this resource when available (Cornwallis, cited in Cramp 1986). Both in Baza and Grao the only fleshy fruit present in appreciable quantities is the Caper, a vine which grows on dry slopes of the ramblas and produces large fruits. Caper fruit constitutes a major food at the end of summer for several different animals inhabiting the two studied zones (Hódar 1993, 1994, 1995, Hódar *et al.* 1996). Caper might be a good and abundant source of fattening just before winter migration for Black-eared Wheatear, but it feeds only rarely on this fruit in Baza.

In conclusion, the Black-eared Wheatear shows an almost strictly insectivorous diet during the reproductive period in the study zones, maintaining this diet even during the fattening period before migration. Its diet is based on ants and grasshoppers, consistently available throughout the study period, other groups being exploited in an opportunistic way when these are abundant. This strategy is quite common among animals living in arid zones (Louw and Seely 1982), in order to confront the low productivity and unpredictable environment that characterises these habitats.

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