

INDIVIDUAL DIET VARIATIONS IN A WINTERING POPULATION OF  
BLACK REDSTART *PHOENICURUS OCHRUIROS*: RELATIONSHIPS  
WITH BIRD MORPHOLOGY AND FOOD AVAILABILITY

José A. HÓDAR\*

Populations are generally considered to be composed not of identical generalist individuals using all available resources in the same way and with similar efficiency, but of morphologically variable individuals that show individual variation in resource exploitation (Via & Lande, 1985). The former variability must produce the latter in a predictable way — that is, if the individual does not choose its diet in an optimal way according to its own morphology, the result is a negative differential fitness (Pyke, 1984; Stephens & Krebs, 1986). One of the basis of ecomorphology is that past natural selection acting on heritable variation has selected the organisms showing the best relationship between morphology and behaviour. Morphological traits usually have a high heritability (Falconer, 1989), and consequently are the raw material for natural selection (Endler, 1986). However, a given individual with fixed morphology can also show variety and flexibility in resource exploitation. These sources of variation in the niche width of a species are referred to as within- (individual flexibility) and between-phenotype (individual differences) (Van Valen & Grant, 1970; Roughgarden, 1972, 1974). Analysis of resource use in this way enables us to separate the proximate, or ecological, factors determining niche width, and the ultimate, or evolutionary, determinants of the mean and variance in the different phenotypes of a given population (Price, 1987).

This path of analysis, however, has been rarely taken into account. In birds, most ecomorphological studies deal with different species, and look for correlations between morphology and resource use of these species (e.g. Carrascal *et al.*, 1990; Landmann & Winding, 1993; Moreno & Carrascal, 1993). This analysis, however, reveals only the consequences of past processes, and not the process itself. Similarly, many authors report individual variation in resource use (e.g. Partridge, 1976; Inman *et al.*, 1987). By contrast, studies matching this variation with morphological characteristics of individuals are surprisingly scarce (Herrera, 1978b; Price, 1987; Gosler, 1987).

A critical question correlating morphology and resource exploitation is the effect of resource supply (Wiens, 1989). Differing efficiencies in resource exploitation will result in differential fitness only in resource-limited situations,

---

\* Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain. E-mail: jhodar@goliat.ugr.es

e.g. food shortage. When food is scarce and the relative abundances of the food types varies, animals must find more quality or quantity of food in order to survive, implying, respectively, a specialization in profitable but scarce resources or a generalist exploitation of all available resources. *A priori*, generalists might be expected to have higher fitness than specialists (Via & Lande, 1985). However, the appearance of specialists in periods of food shortage has been reported elsewhere (Grant & Price, 1981; Schluter *et al.*, 1985; Price, 1987, on Darwin's finches).

In this paper, I address the question of how individual wild birds of a given species confront a situation of food shortage, analysing the relationships between the morphology of each individual and its diet, and taking into account the effect of resource availability. For this study, I have used Black Redstart (*Phoenicurus ochrurus*) wintering in Guadix Basin (southeastern Spain). This species roosts in caves to avoid low nocturnal temperatures: roosts are virtually constant for each bird throughout the winter, allowing a repeated sampling of faeces, a source that offers a representative view of insectivorous bird diet (Ralph *et al.*, 1985). The ecomorphological hypotheses predicts that individual birds with different phenotypes should have different diets according to morphological characteristics. The alternative is that individual birds should be equally generalist, whereupon different phenotypes should show no differences in diet. Furthermore, I analyse the survival advantages of other wintering strategies in relation to the diet choice.

## STUDY AREA

The study was carried out in the Guadix basin (Granada province, southeastern Spain), a Neogene basin composed mainly of clay soils. In low areas appears a bad-land landscape eroded by seasonal watercourses, called "ramblas". Most of the area is dedicated to cereal crops; the vegetation of the ramblas are shrublands with *Salsola oppositifolia*, *Artemisia* spp. and *Retama sphaerocarpa*. The climate, arid continental Mediterranean, has an annual rainfall average of 300 mm with only 55 rainy days per year. During 1990-1992 a mild drought occurred with annual rainfalls of 244, 263 and 336 mm. The average winter temperature fluctuates around 4-6 °C, with an average minimum and maximum of 0 °C and 11 °C, respectively (Castillo-Requena, 1989). Although daytime temperatures can reach nearly 20 °C, sub-zero temperatures are frequently registered at night (as low as -14 °C).

## METHODS

### BIRD SAMPLING PROCEDURE

Throughout December and January in 1990-1991 and 1991-1992, I made nocturnal visits to abandoned caves containing sleeping birds in three zones of the Guadix basin: Fuente Alamo, Hernan Valle and Cuevas del Burrero. In each case, the cave was closed with a sheet and the birds were dazzled with a bright lantern, and then caught by hand or net. Each bird was identified and ringed, and morphological characters were measured. The perch was examined, and corre-

sponding faeces were collected. The faeces were preserved and assigned to the owner of the perch. I discarded samples which were from perches with more than one bird, old or fragmented, at all doubtful in terms of source.

Each cave was usually occupied by only one bird; rarely two or three birds shared a cave. Birds did not change caves or perches when disturbance was minimal, allowing periodic sampling of perches. The most extreme case was an adult female that passed two consecutive winters exactly in the same perch of a cave, and during the third winter, moved only 10 m to the closest cave in the zone, after a total of twelve recaptures.

Morphological measurements of birds included: bill length, from the tip of the bill to the base of the skull; bill depth and width, at the anterior edge of the nostrils; exposed culmen, length of the bill from feathering; rictal bristles; wing length, with the maximum chord method; wing roundness, measured as the distance from the wing tip to the shortest secondary; tail length; tarsus length (bent); hind and middle claw length; and weight (Leisler & Winkler, 1991). Bill, bristles and legs were measured using a digital caliper (precision 0.05 mm); wing and tail with a stop-zero rule (0.5 mm), and weight with a spring scale (0.1 g). Fat deposition was estimated visually in seven classes (0-6) according to Petersson & Hasselquist (1988).

#### DIET DATA

Faeces were dispersed in water and examined with a binocular microscope (10-40x) using an ocular micrometer, identifying prey to the lowest possible taxonomic level. Some prey parts were measured, estimating the size and biomass of the entire prey, by a series of equations developed from a group of arthropods collected in the study area (Hóðar, 1996a, in press). For analysis, diet data were tabulated for each bird, as the frequency of each prey category (number of preys belonging to one category with respect with the total number of preys) both for taxonomic groups and prey size classes.

A diversity-cummulative curve (Magurran, 1988) showed that dietary diversity for each bird was asymptotic in 8-12 samples. Therefore, I have selected 14 birds for individual analysis, those with a minimum of 12 faeces sampled: four from Fuente Alamo, six from Hernan Valle and four from Cuevas del Burrero, all caught the winter 1990-1991.

#### PREY AVAILABILITY

Diet data were compared with availability, measured in four different biotopes in the Guadix basin during the winter of 1990-1991: cereal crops, fallow land, *Salsola-Artemisia* scrubland and *Retama* shrubland. The four biotopes represent usual foraging zones of the Black Redstart in the Guadix area. Twelve unbaited pitfall traps were placed in each biotope every two weeks (48 in total for each biotope). Effectiveness of the pitfall traps depended heavily on arthropod mobility, and thus dormant insects (e.g. Orthoptera) are underestimated, as are groups linked to restricted microhabitats (soil weevils in litter soil, see Discussion) that the Black Redstart can readily find by active search. However, the wintering Black Redstart hunts most of its prey on the ground (Zamora, 1992), and pitfall traps are considered an adequate estimate for soil arthropods as food availability

(Cooper & Whitmore, 1990). Thus, although no method of collecting insects gives an accurate idea about the bird's perception of availability, I chose pitfalls as an appropriate estimate of arthropod availability for the bird in the Guadix Basin during the study period. Arthropods caught in traps were identified to the lowest possible taxonomic level, and their length measured (0.1 mm accuracy). The capture time per sampling was 48 h, but due to the low nocturnal temperatures, arthropod activity was restricted to daytime.

## STATISTICAL PROCEDURES

Concordance between bird prey and arthropod availability was measured using Spearman rank correlation. Before performing the correlations, I removed Acarina and Collembola from availability samples, because these groups were never eaten by the birds. I analysed the preferences of the Black Redstart for the different prey types, according to either taxonomic identity or sizes, using Jacobs' (1974) index *S* of selectivity. The *S* was calculated using availability samples of the four biotopes separately and pooled, both ways giving similar results. Only values with pooled biotope availability are presented.

Principal Components Analysis (PCA) was used to analyse bird biometry and diet (both taxonomy and prey sizes) (Ludwig & Reynolds, 1988). The PCA procedure reduces the original number of variables and allows easier comparisons between the different types of data. I have considered only the axis with the eigenvalue > 1. Prior to all analyses, biometric data were log-transformed, and diet data arcsin transformed, in order to normalize the variables (Zar, 1996). I have not divided lineal bird-biometry variables by cube root of weight to avoid the effect of body size, a procedure usually employed when different species are analysed together. Non-standardized values of variables have a more direct relationship to prey sizes (Carrascal *et al.*, 1990), and within the same species, differences in size can have as much as or even more value than differences in shape among individuals. To investigate the relationship between bird morphology and diet data, I correlated the individual scores of each bird used in the PCA based of biometry (hereafter PCM) with those obtained in prey taxonomy and prey sizes (hereafter PCT and PCS respectively) using the Pearson correlation, with sequential Bonferroni adjustment (Rice, 1989). For prey data, either taxonomy or size, I used each excrement as a unit sample in the PCA analysis; correlations with bird-morphometric scores were made taking the arithmetic mean of diet scores in each axis for all faeces belonging to the same bird. The G log-likelihood test was used to analyse prey taxonomic differences between birds and zones, and nested two-way ANOVA (Zar, 1996), with individual birds nested within zone, for prey-size differences.

## RESULTS

### MORPHOLOGICAL ANALYSIS

Variability in measured morphological variables was diverse, with CV values from 2.3 % to 13.3 % (Table I). Claw, bristle, weight and roundness were the

TABLE I

*Descriptive statistics for the biometry of 14 Black Redstarts selected for diet analysis.  
All measurements in mm except weight, in grams.*

Variables	MEAN	CV	Range
Bill length	16.65	3.79	15.80-17.65
Bill depth	3.20	3.36	3.00-3.35
Bill width	3.39	3.89	3.15-3.60
Culmen	9.74	2.69	9.20-10.10
Bristles	6.35	11.52	5.25-7.95
Wing length	85.65	3.08	80.00-89.00
Wing roundness	19.73	8.92	17.50-22.50
Tail	62.14	4.13	56.00-66.00
Tarsus	23.37	3.74	21.45-24.90
Hind claw	5.85	7.34	5.30-6.80
Middle claw	4.33	13.29	3.65-5.75
Weight	17.25	9.14	15.00-20.00

morphological variables with the largest variation between selected birds. Almost all birds had strong fat reserves (measured as fat state); only two birds exhibited a fat state of 3, whereas 81.3 % (n = 80) scored 5 or 6 (Fig. 1).

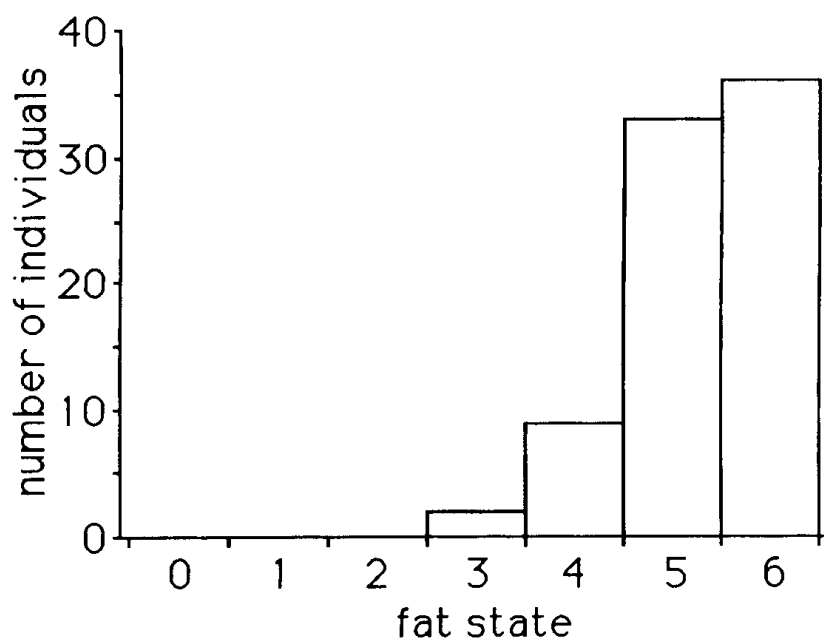


Figure 1. — Fat scores recorded in Black Redstarts wintering in Guadix (n = 80).

PCM reduced 12 variables to 5 axes, with 86.5 % of the total variance (Table II). Bristles, claws and weight were included on the first axis. The second included bill depth and width; third included culmen and tarsus. Wing and tail accounted in fourth axis, and bill length rests in fifth axis.

TABLE II

*Principal component analysis with the twelve biometric variables taken in the 14 Black Redstarts selected for diet analysis, showing the correlations between variables and components.*

Axis	PCM1	PCM2	PCM3	PCM4	PCM5
Eigenvalue	4.06	2.16	1.65	1.29	1.21
% total variance	33.83	51.82	65.59	76.36	86.46
Bill length	- 0.16	- 0.19	0.05	- 0.01	0.92
Bill depth	0.15	- 0.83	0.29	- 0.03	0.27
Bill width	- 0.30	- 0.84	- 0.20	0.22	- 0.04
Culmen	0.25	- 0.26	0.81	- 0.01	- 0.06
Bristles	0.75	- 0.22	0.04	0.29	- 0.42
Wing length	0.27	- 0.09	0.03	0.92	- 0.00
Wing roundness	0.19	0.10	0.17	0.80	- 0.27
Tail	0.12	- 0.20	0.01	0.85	0.27
Tarsus	- 0.10	0.15	0.86	0.16	0.11
Hind claw	0.90	0.01	- 0.09	0.17	- 0.21
Middle claw	0.85	0.25	0.27	0.14	0.07
Weight	0.72	0.09	0.06	0.37	0.51

A total of 193 faeces were analysed (12-17 for each bird), and a total of 1745 prey determined. Worker ants (*Messor* spp., *Camponotus foreli* and *Crematogaster* sp.) were the most abundant prey, with a frequency of 68.9%, and were present in samples of all birds examined (Table III). Curculionidae was the next most consumed prey; these two groups together accounted for 86.1 % of prey frequency in diet. However, these two groups represented on the average only 56.4 % of biomass consumed by birds, although the percentage was highly variable between birds. The other food types, though less frequent, represented 43.6 % of biomass consumed by birds (Table III). There were significant differences between the three zones in the taxonomic composition of diet ( $G = 181.6$ ,  $df = 12$ ,  $p < 0.0001$ ). Similarly, individual birds exhibited differences in their diets ( $G = 618.5$ ,  $df = 65$ ,  $p < 0.0001$ ).

Prey size was estimated for 1339 prey (29-175 for each bird). Prey sizes showed a strong peak between 2 and 4 mm (86.0 % of measured prey), because of the high frequency of worker ants and soil weevils. Differences in prey size showed highly significant differences both for individuals and the bird-excrement interaction (Table IV).

Six PCT axes accounted for 61.5 % of the total variance (Table Va). Formicidae and Curculionidae, the main prey types, appeared on the first axis; only

TABLE III

Prey taxonomy, prey sizes (in mm) and percentage of biomass given by ants, soil weevils and other preys in the 14 Black Redstarts selected for ecomorphological analysis. Availability data are also shown, as prey caught with pitfall traps in the four habitats sampled. FA = Fuente Alamo, H = Hernán Valle, CB = Cuevas del Burro; CER = cereal crop, FAL = fallow land, SCR = Salsola+Artemisia scrubland, RET = Retama shrubland.

Prey taxa	Bird samples										Availability samples									
	FA1	FA2	FA3	FA4	HV1	HV2	HV3	HV4	HV5	HV6	CB1	CB2	CB3	CB4	CER	FAL	SCR	RET		
Araneae	0	0	1	2	0	0	0	0	0	0	0	0	1	1	8	11	4	3		
Myriapoda	0	0	0	0	0	0	0	0	0	0	4	1	2	0	0	1	0	0		
Orthoptera	1	3	14	0	1	0	0	0	2	0	4	5	5	3	0	1	0	0		
Dermoptera	3	2	7	1	0	4	4	4	3	0	2	1	0	0	0	0	2	24		
Lepidoptera L.	0	1	0	0	0	0	0	0	0	10	0	0	0	0	0	1	1	2		
Carabidae	1	2	3	1	0	1	0	0	1	0	0	1	0	0	9	8	5	6		
Tenebrionidae	0	0	0	0	3	1	0	0	0	0	3	0	2	1	0	0	0	0		
Chrysomelidae	0	1	2	0	0	2	0	2	2	0	0	0	2	3	0	2	0	0		
Curculionidae	43	131	10	11	20	9	13	25	16	13	5	3	0	1	4	4	10	9		
Aphodiidae	0	6	0	0	1	1	0	4	3	7	1	0	0	0	2	1	0	0		
Coleoptera oth.	7	1	9	7	7	11	7	0	9	6	9	4	4	2	14	7	5	9		
Formicidae	52	40	79	212	83	76	146	85	95	51	79	67	47	91	3	7	61	63		
Insecta others	1	1	1	2	0	1	1	1	0	0	0	0	0	1	19	23	16	16		
Insecta not eaten	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25	34	24	24		
TOTAL	108	188	126	236	115	106	171	121	131	87	107	82	63	103	84	100	135	156		
Prey size classes																				
0-2.0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	4	12	4	3		
2.1-4.0	70	158	72	168	82	68	138	84	89	58	63	43	21	38	29	13	58	46		
4.1-6.0	8	11	2	4	4	3	2	8	11	7	8	9	2	9	19	21	32	41		
6.1-8.0	1	1	2	1	0	2	1	3	4	1	0	0	3	2	3	9	11	31		
8.1-10.0	0	0	0	1	0	0	0	1	0	0	0	2	0	0	2	3	1	3		
10.1-14.0	3	0	1	1	0	1	3	3	3	1	6	2	0	2	3	7	1	3		
14.1-20.0	0	3	2	0	0	3	1	1	3	6	2	1	2	1	1	1	4	4		
> 20.1	0	2	9	0	1	0	0	0	0	3	1	3	0	1	0	0	0	1		
TOTAL	83	175	88	175	87	77	145	100	110	76	81	60	29	53	59	66	111	132		
% biomass ants+weevils	58	50	6	83	45	41	76	80	53	25	24	27	12	33						
% biomass others	42	50	94	17	55	59	24	20	47	75	76	73	82	67						

TABLE IV

*Nested two-way ANOVA of prey length in the 14 Black Redstarts selected for diet analysis.*

Source of variation	df	Sum of Squares	Mean of Squares	F-ratio	P-value
Excrement	1	0.001	0.004	0.087	0.7682
Zone	2	0.212	0.106	2.387	0.0928
Bird × Excrement	13	1.710	0.132	2.995	0.0003
Bird (Zone)	11	1.550	0.141	3.116	0.0003
Residual	1 317	58.621	0.045		

TABLE V

*Principal components analysis with the 13 taxonomic prey groups (A) and 8 prey size classes (B) recognized in the diet of 14 Black Redstarts selected for diet analysis, showing the correlations between variables and components. Prey size class in mm.*

**A**

Axis	PCT1	PCT2	PCT3	PCT4	PCT5	PCT6
Eigenvalue	1.79	1.49	1.29	1.21	1.17	1.06
% total variance	13.75	25.17	35.07	44.40	53.40	61.53
Araneae	0.11	0.03	-0.04	0.09	0.72	-0.01
Myriapoda	0.02	0.02	0.08	0.68	-0.12	0.21
Caelifera	-0.12	0.26	-0.02	0.24	-0.33	0.54
Dermaptera	-0.31	0.08	0.10	-0.03	0.71	0.06
Lepidoptera Larv.	-0.13	-0.75	0.07	-0.05	-0.09	0.02
Carabidae	-0.08	-0.03	-0.78	-0.02	-0.07	0.18
Tenebrionidae	0.08	0.05	-0.76	-0.07	0.03	-0.19
Chrysomelidae	-0.30	0.32	0.07	-0.30	0.03	0.32
Curculionidae	-0.76	-0.14	0.14	-0.19	-0.09	-0.12
Aphodiidae	-0.04	-0.75	-0.04	-0.02	0.01	0.02
Coleoptera others	-0.04	0.06	0.03	0.74	0.23	0.19
Formicidae	0.88	0.02	0.21	-0.30	-0.25	-0.01
Insecta others	-0.23	0.24	0.01	0.07	-0.22	-0.72

**B**

Axis	PCS1	PCS2	PCS3	PCS4	PCS5
Eigenvalue	1.73	1.21	1.14	1.09	1.03
% total variance	21.63	36.70	51.01	64.59	77.50
0-2.0	-0.04	-0.08	-0.02	0.98	-0.04
2.1-4.0	-0.79	-0.34	-0.26	-0.32	-0.29
4.1-6.0	0.77	-0.23	0.11	-0.10	-0.08
6.1-8.0	0.08	0.03	0.91	-0.04	-0.04
8.1-10.0	0.60	0.14	-0.41	-0.12	-0.06
10.1-14.0	0.08	0.78	-0.14	0.09	-0.14
14.1-20.0	-0.07	0.67	0.14	-0.18	0.13
> 20	0.01	-0.02	-0.03	-0.04	0.99



Chrysomelidae did not appear on any axis. Five PCS axes accounted for 77.5 % of the total variance (Table Vb), and the three main size classes were included in the first axis.

#### RELATIONSHIP DIET-AVAILABILITY

Concordance between diet and availability was found especially with data from the *Salsola-Artemisia* scrubland (4 birds with  $p < 0.05$  in taxonomy and 4 in size distribution) and the *Retama* shrubland (3 and 6), whereas concordance with cereal crops and fallow land were rare, either in taxonomy (1 and 1) or in sizes (1 and 1, respectively). Only one bird showed no correlation with  $p < 0.10$ .

Selectivity showed positive values for Formicidae and size class 2.1-4.0 mm (Table VI); Orthoptera, Curculionidae and large prey sizes showed values close to 0. All other groups given negative values of  $S$ . Nevertheless, the average selectivity values for selected birds contrasted with selectivities calculated after pooling the diet of the same birds. Pooled data generally offered higher values of selectivities than did average values (Table VI). The distribution of  $S$ 's individual values for all birds is plotted in Fig. 2. The presence of only a modal class in  $-1.0$

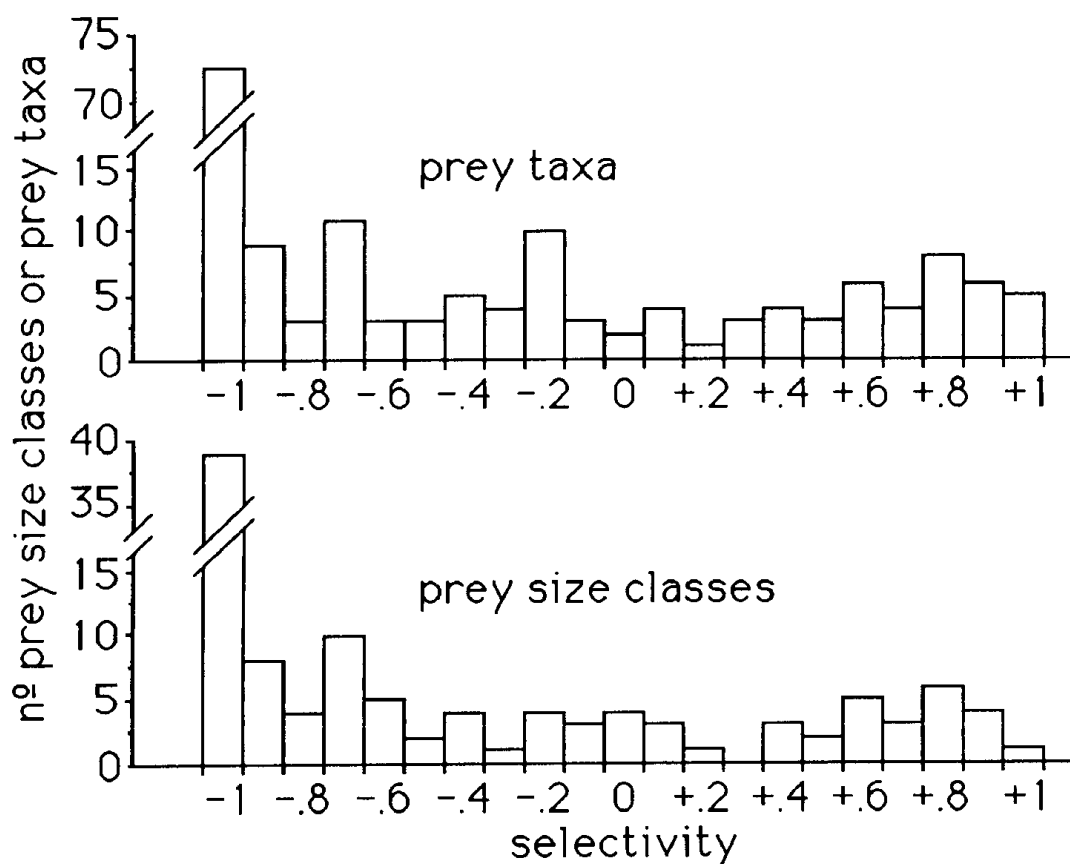


Figure 2. — Plotted values of selectivity for the 14 Black Redstarts selected for diet analysis.

indicates rejection through different individuals of several prey classes. Values up to 0 are rare, almost restricted to worker ants, and variation among individuals in prey selection is substantial (see SD values in Table VI).

TABLE VI

*Selectivity values (Jacobs' S index) obtained with pooled availability data. Left column offers mean and standard deviation of the values obtained in each of 14 Black Redstarts selected for diet analysis, right column offers the values obtained pooling the diet of all birds. Tenebrionidae was pooled with other Coleoptera, because no beetle of this family was caught in pitfall traps. Prey size class in mm.*

Group/size class	mean $\pm$ SD	Pooled
Araneae	$-0.93 \pm 0.12$	-0.93
Myriapoda	$-0.64 \pm 0.72$	-0.05
Orthoptera	$0.17 \pm 0.91$	0.82
Dermaptera	$-0.61 \pm 0.33$	-0.55
Lepidoptera Larv.	$-0.84 \pm 0.49$	-0.43
Carabidae	$-0.87 \pm 0.16$	-0.85
Chrysomelidae	$-0.35 \pm 0.70$	-0.05
Curculionidae	$0.10 \pm 0.56$	0.49
Aphodiidae	$-0.70 \pm 0.40$	-0.60
Coleoptera others	$-0.35 \pm 0.33$	-0.35
Formicidae	$0.63 \pm 0.30$	0.66
Insecta others	$-0.97 \pm 0.03$	0.96
0.0-2.0	$-0.96 \pm 0.10$	-0.96
2.1-4.0	$0.78 \pm 0.12$	0.82
4.1-6.0	$-0.68 \pm 0.18$	-0.71
6.1-8.0	$-0.81 \pm 0.20$	-0.85
8.1-10.0	$-0.86 \pm 0.32$	-0.80
10.1-14.0	$-0.36 \pm 0.45$	-0.27
14.1-20.0	$-0.26 \pm 0.53$	-0.12
> 20.1	$-0.14 \pm 0.87$	0.54

#### RELATIONSHIP DIET-MORPHOLOGY

The scores of birds in the five morphological axes PCM1-PCM5 were correlated with the mean bird scores in the six axes of taxonomic prey PCT1-PCT6 and the five axes of prey size PCS1-PCS5, and also with the mean and the standard deviation of prey length, and Shannon diversity index of taxonomy and prey size for each individual bird. Only five out of 75 correlation tests were significant with  $p < 0.05$ , a figure included in the 5 % expected by random ( $\chi^2 = 0.58$ ,  $p = 0.46$ ,  $df = 1$ ). In fact, significant correlations were discarded as spurious after correction with sequential Bonferroni, and none of the correlations performed could be considered significant, even at  $\alpha = 0.10$  table level.

## DISCUSSION

The foraging pattern of Black Redstart wintering in Guadix basin corresponds to a nonselective, generalist feeder. It shows a high foraging rate of about 7.7 captures/min, and completely, and apparently with ease, changes its summer foraging pattern: from mainly perch-gleaning and aerial hawking, to ground-gleaning and perch-to ground sallying in winter (Zamora, 1992). These features contrast with the results reported here. High foraging rate suggests that prey consumed must have a high encounter rate, in contrast with availability data that indicate a general low prey availability. In the same way, short searching periods between consecutive prey suggest low selectivity in prey choice, type or size (Zamora, 1992), in contrast with the selectivity analysis, which indicates rejection of most groups, and selection of ants and few others. Individual birds had different diets (Tables III and IV), consistently selected several types of prey (Fig. 2) and showed individual differences in selection patterns (Table VI). There was morphological variation in birds (Table I), but not correlation between this morphological variation and the diet features.

To explain these results, an analysis of the abiotic conditions for wintering in Guadix is needed. The Guadix-Baza basin in winter undergoes a strong temperature inversion, in which cold air due to nocturnal radiant cooling drains from the mountains to the basin. This produces mild days but hard nocturnal freezes throughout the winter, only rarely broken by short and unpredictable stormy periods (Castillo-Requena, 1989). Bare ground in most biotopes, in combination with harsh weather, results in difficult living conditions for arthropods, with temperatures allowing activity during day but lethal at night (Bale, 1991; Block, 1991). For strictly insectivorous birds, sunny days usually provide good foraging conditions all day, but a scarcity of arthropods and low nocturnal temperatures represent strong handicaps for survival. As a consequence, the challenge that each bird must face every day is to obtain enough food by maximizing the foraging rate or to find high-quality prey, and overnight at low temperatures with minimum energetic costs.

To obtain enough food, the Black Redstart bases its diet upon ants and soil weevils, and takes other prey when found. Ants construct their nests underground, providing a nocturnal refuge against freezing (Bale, 1991) and allowing diurnal activity when the sun warms the environment. The high number of individuals per colony and conspicuousness of nests make worker ants an easy target, reducing the Black Redstart's searching time. Furthermore, Black Redstarts are residents and sometimes territorial while wintering (Zamora, 1992; Cuadrado, 1995), and such permanence in a known area makes it easy for the bird to learn the location of ant-nests. Soil weevils, the other main prey, are abundant in the soil during the winter, mainly in *Medicago* spp. litter (personal observation), but low mobility makes this insect difficult to record in pitfall traps. Both ant nests and soil litter are rare in cereal crops and fallow lands because of agricultural tilling, but are common in *Salsola-Artemisia* scrublands and *Retama* shrublands, the natural habitats of the basin. This explains the most significant correlations between availability and diet within these two biotopes, in which the Black Redstart reaches its highest winter densities (up to 6 birds/10 ha against 0.05-0.5 birds/10 ha in cereal crops and fallow lands, Hódar, 1996b, c).

It is already known that insectivorous birds use ants as alternative food resource during winter, but these insects have been described as suboptimal prey

to be used only in emergencies. Herrera (1983, see also 1978a) found ants to be a major source of food for a variety of wintering insectivores in southern Spain, the Black Redstart among them, but these bird species shift to more profitable prey when available. However, the data of biomass consumption (Table III) suggest a different view than the frequency data. The numerical basis of the diet is small, highly sclerotized, unprofitable prey like worker ants and weevils, but a main food source are large, highly profitable prey like Orthoptera or Dermaptera, which are consumed when found; even millipedes are consumed despite their deterrents.

To overnight while minimizing energetical costs, the Black Redstart roosts in caves. For a small bird, with high thermoregulatory costs, winter roosting is highly expensive due to long nights and low temperatures. Sheltered roosting can represent, in energetic terms, a 40 % saving compared to outdoor roosting (Calder & King, 1975; Walsberg, 1985). In the Guadix Basin, other species such as the Black Wheatear (*Oenanthe leucura*), the Rock Sparrow (*Petronia petronia*) and the Tree Sparrow (*Passer montanus*), share the caves with the Black Redstart, taking advantage of the shelter. In nearby zones without caves, the Black Redstart looks for other protected roost sites such as abandoned farms or natural shelters (personal observation).

However, these two strategies do not work during the scarce and unpredictable stormy and rainy periods, in which foraging is impossible. The Black Redstart needs to accumulate fat reserves for lean periods throughout the winter (Ekman & Hake, 1990; Bednekoff *et al.*, 1994; Lovvorn, 1994). In fact, fat scores in Guadix are much higher ( $5.3 \pm 0.1$ , Fig. 2) than recorded in other populations of Black Redstart wintering in milder zones (2.5 to 3.4 in Cuadrado 1995). However, the accumulation of reserves requires extra food, and this necessity is the key to explaining the lack of correlation between morphology and diet. When food is scarce but the food types are predictable, birds with higher efficiency in the more predictable food types have a better chance for survival, whereas individuals with an intermediate performance between two food types are disadvantaged (see e.g. Price, 1987). For the Black Redstart in Guadix, the predictable and numerically important prey are ant workers and soil weevils, small and unprofitable prey, whereas large prey, which represent roughly a half of the biomass consumed, are scant and unpredictable. To overwinter, an individual Black Redstart cannot specialize on one or another kind of prey — it needs both. The effect of this bipolarization is shown in the selectivity values for prey size classes (Table VI): only 2.1–4.0 mm (ants and weevils) and up to 10 mm (big prey) have values close or up to 0.

These differences in taxonomy, size, availability and predictability of the two basic kinds of prey do not allow to Black Redstart any possibility for individual specialization. When resources are limited, individual birds in particular, and animals in general, must choose, according to their morphology, between a generalist use of all the scarce resources, or an efficient and specialized use of the best available resources. The second path matches morphology to ecology (Gosler 1987; Price, 1987), but sometimes, as with the Black Redstart wintering in Guadix, the first is the only path available.

#### ACKNOWLEDGEMENTS

Regino Zamora encouraged me in several ways and in all the stages of development of this work. Mariano Cuadrado, José M. Gómez, Benja Rosales,

Juanfra Sánchez-Casado, Paco Sánchez-Piñero and some others helped me during the redstart's capture. John P. Ball, J.M. Gómez, Anthony Joern, Mats Lindén, F. Spitz, R. Zamora and an anonymous referee criticized several earlier versions of this manuscript, giving valuable suggestions. David Nesbitt kindly improved the English. Lodging for field work was provided by the Confederación Hidrográfica del Guadalquivir (especially D. José Hernández) and the direction of Parque Natural Sierra de Baza. During this work, I was supported by a grant PFPI from Spanish Ministerio de Educación y Ciencia.

## SUMMARY

Ecomorphology in birds has usually centered on the analysis of closely related species, and only seldom has focused on individual differences within species. In the present study, I used the Black Redstart *Phoenicurus ochruros* to analyse the main assumption of ecomorphological hypothesis - that is, the correlation between morphology and ecology, on an individual level. I collected both biometric data and faecal samples from 14 selected individuals in a winter population of the Guadix Basin (SE Spain), in which birds overwinter while enduring harsh climatic conditions and food scarcity. I analysed individual correlations between morphology and diet, as well as individual differences in diet selection according to availability. Diet data were highly variable between individual birds, though always based on worker ants and soil weevils, and in general showed no significant similarity with availability data. Also, birds showed individual differences in selectivity patterns. However, there was little correlation between morphological bird traits and prey characteristics. Individual birds based their diet on ants and weevils, ate other prey when found, and used sheltered roosts in order to maintain high fat stores with which to survive unpredictable wintering conditions. I suggest that the scarcity and low quality of available prey in this area force Black Redstart to display a generalist foraging strategy, and do not allow individual specialization in any prey type.

## RÉSUMÉ

Chez les oiseaux, les études écomorphologiques se sont en général focalisées sur l'analyse d'espèces étroitement apparentées, plus rarement sur les différences individuelles infraspécifiques. Le présent travail, relatif au Rougequeue noir *Phoenicurus ochruros*, analyse la principale hypothèse de la théorie écomorphologique, à savoir l'existence d'une corrélation au niveau de l'individu entre morphologie et écologie. Des données biométriques et des échantillons de fèces ont été recueillis sur 14 individus d'une population hivernale du bassin de Guadix (sud-est de l'Espagne) où les oiseaux hivernent, éprouvant des conditions climatiques difficiles et une nourriture raréfiée. Les données relatives au régime alimentaire variaient fortement entre les individus bien que soulignant toujours une base de fourmis et de charançons du sol et, en général, ne montraient aucune relation significative avec les données sur la disponibilité de la nourriture. Les oiseaux affichaient également des différences individuelles dans leurs patrons de sélection des proies. Toutefois, la corrélation était faible entre les traits morpho-

logiques des oiseaux et les caractéristiques des proies. Les individus fondaient leur régime alimentaire sur les fourmis et les charançons, consommant d'autres proies au fil des rencontres et utilisant des reposoirs protégés afin de maintenir de fortes réserves adipeuses leur permettant de survivre dans des conditions hivernales imprévisibles. Il est suggéré que la rareté et la faible qualité des proies disponibles dans la région d'une part forcent le Rougequeue noir à se comporter en généraliste dans sa stratégie d'approvisionnement alimentaire et, d'autre part, n'autorisent aucune spécialisation individuelle sur un quelconque type de proie.

## REFERENCES

- BALE, J.S. (1991). — Insects at low temperature: a predictable relationship? *Funct. Ecol.*, 5: 291-298.
- BEDNEKOFF, P.A., BIEBACH, H. & KREBS, J. (1994). — Great tit fat reserves under unpredictable temperatures. *J. Avian Biol.*, 25: 156-160.
- BOCK, W. (1991). — To freeze or not to freeze? Invertebrate survival of sub-zero temperatures. *Funct. Ecol.*, 5: 284-290.
- CALDER, W.A. & KING, J.R. (1975). — Thermal and caloric relations of birds. pp. 259-413 in Farner, D.S. and King, J.R. (eds.). *Avian Biology*, 4. Academic Press, New York.
- CARRASCAL, L.M., MORENO, E. & TELLERÍA, J.L. (1990). — Ecomorphological relationships in a group of insectivorous birds of temperate forests in winter. *Holarct. Ecol.*, 13: 105-111.
- CASTILLO-REQUENA, J.M. (1989). — *El clima de Andalucía: clasificación y análisis regional con los tipos de tiempo*. Col. Investigación nº 13, I.E.A., Almería.
- COOPER, R.J. & WHITMORE, R.C. (1990). — Arthropod sampling methods in ornithology. *Stud. Avian Biol.*, 13: 29-37.
- CUADRADO, M. (1995). — Winter territoriality in migrant Black Redstarts *Phoenicurus ochruros* in the Mediterranean area. *Bird Study*, 42: 232-239.
- EKMAN, J.B. & HAKE, M.K. (1990). — Monitoring starvation risk: adjustment of body reserves in Greenfinch (*Carduelis chloris* L.) during periods of unpredictable foraging success. *Behav. Ecol.*, 1: 62-67.
- ENDLER, J.A. (1986). — *Natural selection in the wild*. Princeton Univ. Press, Princeton.
- FALCONER, D.S. (1989). — *Introduction to quantitative genetics*. Longman Sci. Techn. Essex.
- GOSLER, A.G. (1987). — Pattern and process in the bill morphology of the Great Tit *Parus major*. *Ibis*, 129: 451-476.
- GRANT, P.R. & PRICE, T.D. (1981). — Population variation in continuously varying traits as an ecological genetics problem. *Amer. Zool.*, 21: 795-811.
- HERRERA, C.M. (1978a). — Datos sobre la dieta invernal del Colirrojo Tizón (*Phoenicurus ochruros*) en encinares de Andalucía Occidental. *Doñana Acta Vert.*, 5: 61-71.
- HERRERA, C.M. (1978b). — Individual dietary differences associated with morphological variation in Robins *Erithacus rubecula*. *Ibis*, 120: 542-545.
- HERRERA, C.M. (1983). — Significance of ants in the diet of insectivorous birds in southern Spanish mediterranean habitats. *Ardeola*, 30: 77-84.
- HÓDAR, J.A. (1996a). — The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecol.*, 17: 421-433.
- HÓDAR, J.A. (1996b). — Seasonal variations in two shrubsteppe bird assemblages in southeastern Spain: the importance of wintering for non-steppe birds pp. 137-151 in: Fernandez, J. & Sanz-Zuasti, J. (eds.). *Proc. Int. Symp. on Conserv. of Steppe birds and their Habitat*, Junta de Castilla y León, Valladolid.
- HÓDAR, J.A. (1996c). — Temporal variations in two cereal crop bird assemblages in southeastern Spain pp. 173-181 in: Fernandez, J. & SANZ-ZUASTI, J. (eds.). *Proc. Int. Symp. Conserv. of Steppe birds and their Habitat*, Junta de Castilla y León, Valladolid.
- HÓDAR, J.A. (in press). — The use and usefulness of regression equations for estimation of prey length and biomass in diet studies of insectivore vertebrates. *Miscellanea Zoológica*.
- INMAN, A.J., LEFEBVRE, L. & GIRALDEAU, L.A. (1987). — Individual diet differences in feral pigeon: evidence for resource partitioning. *Anim. Behav.*, 35: 1902-1903.
- JACOBS, J. (1974). — Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. *Oecologia*, 14: 413-417.
- LANDMANN, A. & WINDING, N. (1993). — Niche segregation in high-altitude Himalayan chats (Aves, Turdidae): does morphology match ecology? *Oecologia*, 95: 506-519.

- LEISLER, B. & WINKLER, H. (1991). — Ergebnisse und Konzepte ökomorphologischer untersuchungen an Vögeln. *J. Ornithol.*, 132: 373-425.
- LOVVORN, J.R. (1994). — Nutrient reserves, probability of cold spells and the question of reserve regulation in wintering canvasbacks. *J. Anim. Ecol.*, 63: 11-23.
- LUDWIG, J.A. & REYNOLDS, J.F. (1988). — *Statistical ecology*. John Wiley & Sons, New York.
- MAGURRAN, A.E. (1988). — *Ecological diversity and its measurement*. Croom Helm, London.
- MORENO, E. & CARRASCAL, L.M. (1993). — Leg morphology and feeding postures in four *Parus* species: an experimental ecomorphological approach. *Ecology*, 74: 2037-2044.
- PARTRIDGE, L. (1976). — Individual differences in feeding efficiencies and feeding preferences of captive Great Tits. *Anim. Behav.*, 24: 230-240.
- PETERSSON, J. & HASSELQUIST, D. (1985). — Fat deposition and migration capacity of Robins *Erithacus rubecula* and Goldcrest *Regulus regulus* at Ottenby, Sweden. *Ringing and Migration*, 6: 66-76.
- PRICE, T. (1987). — Diet variation in a population of Darwin's finches. *Ecology*, 68: 1015-1028.
- PYKE, G.H. (1984). — Optimal foraging theory: a critical review. *Ann. Rev. Ecol. Syst.*, 15: 523-575.
- RALPH, C.P., NAGATA, S.E. & RALPH, C.J. (1985). — Analysis of droppings to describe diets of small birds. *J. Field Ornithol.*, 56: 165-174.
- RICE, W.R. (1989). — Analysing tables of statistical tests. *Evolution*, 43: 223-225.
- ROUGHGARDEN, J. (1972). — Evolution of niche width. *Am. Nat.*, 106: 683-718.
- ROUGHGARDEN, J. (1974). — Niche width: biogeographical patterns among *Anolis* lizards populations. *Am. Nat.*, 108: 429-442.
- SCHLUTER, D., PRICE, T.D. & GRANT, P.R. (1985). — Ecological character displacement in Darwin's finches. *Science*, 227: 1056-1059.
- STEPHENS, D.W. & KREBS, C.J. (1987). — *Foraging theory*. Princeton U. P., Princeton.
- VAN VALEN, L. & GRANT, P.R. (1970). — Variation and niche width reexamined. *Am. Nat.*, 104: 589-590.
- VIA, S. & LANDE, R. (1985). — Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution*, 39: 505-522.
- WALSBERG, G.E. (1985). — Physiological consequences of microhabitat selection pp. 389-413 in: Cody, M.L. (ed.). *Habitat selection in birds*. Academic Press, London.
- WIENS, J.A. (1989). — *The ecology of bird communities*, vol. 1. Cambridge U. P., Cambridge.
- ZAMORA, R. (1992). — Seasonal variations in foraging behaviour and substrate use by the Black Redstart (*Phoenicurus ochruros*). *Rev. Ecol. (Terre Vie)*, 47: 67-84.
- ZAR, J.H. (1996). — *Biostatistical analysis*, 3rd ed. Prentice-Hall, New Jersey.