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SEASONAL VARIATIONS IN FORAGING BEHAVIOUR
AND SUBSTRATE USE BY THE BLACK REDSTART
(*PHOENICURUS OCHRUIROS*)

Regino ZAMORA*

Theoretical and empirical studies indicate that predators search for prey in two exclusive ways, namely active searching (i.e. when the predator actively looks for prey) and passive searching (i.e. when the predator is waiting for a mobile prey, see MacArthur and Pianka 1966, Schoener 1969, Eckhardt 1979 and Huey and Pianka 1981 for reviews). This bimodality in predator search modes has recently been formalized in the so-called « Syndrome Hypothesis » (Eckhardt, 1979 ; McLaughlin, 1989), which proposes that active and passive searching are species-specific strategies, and that each strategy represents a syndrome of co-evolved behavioural and eco-morphological characters. There are indications, however, that some predators switch between sit-and-wait and active search tactics (Davies, 1977 ; Paszkowski, 1982 ; Pietruzka, 1986). Very little is known about intraspecific variability, because most studies exclusively consider interspecific differences between and within guilds (e.g. Eckhardt, 1979 ; Huey and Pianka, 1981).

Forest insectivorous birds have been extensively used to test predator strategies, although this information has been obtained almost exclusively during the breeding season (see the review of McLaughlin, 1989). Such a limited approach in the majority of studies gives an incomplete and biased view of the actual situation, because many species change their feeding behaviour and habitat use during the seasonal cycle (e.g. Alatalo, 1980 ; Rice *et al.*, 1980 ; Wagner, 1981 ; Hutto, 1985 ; Morrison *et al.*, 1986). These changes manifest themselves more clearly in the case of migratory birds, which occupy distinct habitats during the breeding and wintering seasons (see Root, 1967 ; Baker and Baker, 1973 ; Bennett, 1980 ; Rabenold, 1980 ; Hutto, 1981).

Many high-mountain birds are migratory, spending part of the yearly cycle in habitats that are very different from the mountains where they breed. This is the case for the Black Redstart (*Phoenicurus ochruros*), a small insectivorous passerine that may be considered as a « generalist » as far as its morphology (Zamora, 1988a) and ecology are concerned (Zamora, 1990). This species breeds in mediterranean and temperate European mountains, and occupies a wide altitudinal range in the Sierra Nevada of southern Spain (Zamora, 1987), reaching its

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greatest density in rocky habitats situated between 2 000 and 2 500 m a.s.l. (Zamora, 1988b, 1991). In fall, it moves at lower elevations, to winter in a variety of habitats (Zamora *et al.*, 1987 ; Zúñiga *et al.*, 1987).

In this paper, I intend to test the « Syndrome Hypothesis » of predator search modes on an open-habitat migratory bird, the Black Redstart. I focus my analysis on the seasonal differences in foraging behaviour in relation to habitat structure and prey availability, in both breeding and wintering habitats. This should enable me to establish whether the Black Redstart switches its tactics between sit-and-wait and active search modes or has a fixed species-specific search strategy (McLaughlin, 1989).

I. — STUDY AREA

The study was carried out in the province of Granada, southern Spain, in two locations representative of the breeding and wintering habitats of the Black Redstart :

a) *Breeding habitat* : The study area was located between 2 200 and 2 400 m on the northern slope of the Sierra Nevada. *Juniperus communis* and *Genista baetica* were the principal shrub species (see Table VI for cover percentages). The height of the shrub layer rarely exceeded 60 cm, and the shrubbery was intermingled with rocks, grasses and bare ground. A more detailed description of the habitat can be found in Zamora (1988b). The area remained snow-covered for 5-7 months each year, usually between November and April. The mean temperature during May-September was 13 °C.

b) *Wintering habitat* : The winter study area was located in the Rambla del Grao (Guadix Depression). Here, the landscape is typical of the « bad-lands » resulting from fluvial erosion on muddy substrates. The observations were carried out in a seasonal watercourse area, situated at a 1 000 m elevation. The shrub vegetation was composed by *Retama sphaerocarpa*, *Salsola phloskae* and *Artemisia sp.* (See Table VI for cover percentages). The height of the shrub layer did not exceed 3 m (Zamora *et al.*, 1987). The mean winter temperature was 5 °C, with frequent night frosts.

Habitat characteristics were recorded at sampling points located randomly within both the breeding (n = 255) and wintering (n = 280) study areas. The substrate coverage was determined at each sample point following Wiens and Rotenberry's (1981) procedure (see also Zamora, 1988b).

II. — METHODS

1. *Prey availability*

Arthropod availability was quantified on the ground, in the shrubs and in the air, in both breeding and wintering study areas, using the same sampling protocol. Terrestrial arthropods were sampled by means of 20 pit-fall traps (6.4 cm in diameter). The availability of arthropods in the shrub layer and in the air was estimated by means of 20 adhesive traps (sticky boards of 3.15 dm²) ; 10 placed

into the shrubs and 10 hanging from them. These traps were set twice each month in both habitats. The capture period of the traps (pit-falls and sticky boards) was 48 h.

2. Feeding ecology

I moved systematically over each study area and, when a foraging bird was encountered, I recorded its actions on a portable tape recorder. I noted the search strategies, prey-capture techniques and substrate use, recording being limited to 5 min per individual sequence. Long recordings provide a more accurate description of the behaviour of ground-foraging birds (Holmes and Robinson, 1984), especially when they search from a perch (e.g. Greig-Smith, 1984 ; Moreno, 1984 ; Zamora, 1990). Routes were alternated between days, and no individual bird was observed more than once per day. Days when particularly inclement weather might have affected the normal foraging habits of the birds were avoided (Grubb, 1977, 1978). The prey-capture techniques were categorized following Fitzpatrick's (1980) definitions: perch-to-ground sallying, aerial hawking, gleaning, sally-gleaning, and ground-foraging. A particular case of ground-foraging is probe (Holmes and Robinson, 1988), when a bird's beak enters the ground surface to reach prey.

The following foraging substrates were distinguished: ground (bare ground or ground with some grass), rock, shrub (*J. communis*, *G. baetica* and *Ptilotrichum spinosum* in Sierra Nevada ; *Retama sphaerocarpa*, *Salsola phloskiae* and *Artemisia* sp. in Guadix) and air. I also noted the characteristics, and estimated the height (to the nearest 10 cm interval) of the perch used. Distances from perch base to landing point on the ground, as well as the distances covered during the search for prey were roughly estimated.

The data obtained in both breeding and wintering habitats were divided into four periods: spring, summer (S. Nevada), fall, and winter (Guadix). I conducted comparisons at two levels: 1) between breeding and wintering habitats as a whole; 2) within habitats (spring-summer, and fall-winter). The duration of each period was: spring (from May to 20 July, 1985), which corresponds to the breeding season; summer (from 20 July to 15 September, 1985); fall (October and November, 1985), and winter (December, 1985 and January, 1986). I retained for analysis only sequences > 30 s in length. The number of feeding sequences obtained in each period was: spring = 112, summer = 104, fall = 82, winter = 57. Only adult birds were observed, and both males and females were equally represented in the data set. A minimum of 16 (breeding habitat) and 20 (wintering habitat) individual Black Redstarts were represented. The number of individuals were estimated by means of transect counts in the same study areas (see Zamora, 1988b and Zamora *et al.*, 1987 for density data).

The niche breadth and niche overlap were respectively calculated by means of Levins' (1968) and Schoener's (1968) indices. All statistical tests were taken from Siegel (1956) and Zar (1984).

III. — RESULTS

The Black Redstart alternates short movements (« within-patch ») with long movements (« between-patches ») when searching for prey. The radial distance

which defines the patch is about 10 m, corresponding to the maximum capture distance observed. The greater patch-change frequency occurs during spring and fall (Table I). The Black Redstart moves much more in spring than in summer ($U = 341$, $p < 0.05$, Mann-Whitney U test), whereas there are no statistically significant differences between fall and winter ($U = 187$, $p > 0.05$), and between breeding and wintering habitats as a whole ($Z = 1.19$, $p > 0.05$, Mann-Whitney U test, normal approximation). The seasonal comparison of the move rates shows a lack of difference between spring and summer ($U = 204$, $p > 0.05$), and between fall and winter ($U = 190$, $p > 0.05$), whereas significant differences do exist between the breeding and wintering habitats as a whole ($Z = 2.96$, $p = 0.001$). The differences in rate of travel are related to the within-patch locomotion pattern, which is essentially aerial in Sierra Nevada, and both pedal and aerial in Guadix (Table I).

TABLE I

Some general search-strategy features of the Black Redstart.

Patch-change frequency is the mean number of uninterrupted flights of more than 10 m per h of observation. The mode of locomotion (%) in a patch may be either aerial or pedal. Rate of travel is the distance covered (m/min) within a patch. Move rate is the mean number of changes of location when looking for prey per minute. Prey-capture rate is the mean number of prey-capture attempts per minute. The data for Rate of travel, Move rate and Prey-capture rate are $\bar{X} \pm (SD)$.

	Spring	Summer	OVERALL S. NEVADA	Fall	Winter	OVERALL GUADIX
Patch-change frequency	28.3	13.7	19.9	28.6	15.9	21.0
Aerial locomotion	92.0	82.5	87.8	68.1	40.9	46.4
Pedal locomotion	8.0	17.5	12.2	31.9	59.1	53.6
Rate of travel	24.2(10.0)	12.3(4.9)	18.1(9.8)	15.7(8.1)	13.1(4.6)	14.4(6.6)
Move rate	13.6(4.4)	13.7(3.7)	13.7(4)	15.0(6.5)	19.3(8.6)	17.2(7.6)
Prey-capture rate	5.4(2.4)	4.8(1.7)	5.1(2)	6.3(4.0)	7.7(2.7)	7.0(3.5)

The prey-capture rate is significantly greater in Guadix than in Sierra Nevada ($Z = 1.64$, $p = 0.05$), whereas significant differences do not appear between spring and summer ($U = 217.5$, $p > 0.05$) and fall and winter ($U = 196$, $p > 0.05$).

The Black Redstart uses five prey-capture techniques in Sierra Nevada (Table II), four of which are employed in similar proportions (perch-to-ground sallying, aerial hawking, gleaning and ground foraging). In contrast, ground foraging and perch-to-ground sallying are the main techniques in the wintering habitat. In Guadix, the Black Redstart also captures some prey by probing the ground with its beak (probe), a technique never employed in the Sierra Nevada. The values of the G-test (Table II) clearly demonstrate that the inter-habitat

TABLE II

Percentage of observations within each of the six foraging categories.

Sample size (N) is the number of prey-capture attempts. $1/\Sigma \pi_i^2$ = niche breadth values. The G-test values for the comparisons spring-summer, fall-winter and Overall S. Nevada-Overall Guadix (the latter under the heading Overall S. Nevada) are also shown. * = $p < 0.001$.

	Spring	Summer	OVERALL S. NEVADA	Fall	Winter	OVERALL GUADIX
Probe	0.0	0.0	0.0	8.5	5.8	7.0
Ground-foraging	19.6	24.9	23.0	59.9	64.6	62.5
Perch-to-ground	25.7	29.3	27.9	28.2	27.4	27.8
Gleaning	23.6	24.8	24.3	0.2	0.0	0.1
Sally-gleaning	10.0	4.2	6.3	0.6	0.2	0.4
Aerial-hawking	21.0	16.7	18.3	2.4	0.2	2.2
N	627	1081	1708	457	554	1011
$1/\Sigma \pi_i^2$	4.66	4.17	4.38	2.24	2.01	2.11
G-test	32.2*		6919.2*	6.8,ns		

differences are much larger than the temporal differences within habitats, although significant differences also appear between spring and summer.

In Sierra Nevada there is a greater abundance of arthropods than in Guadix : they are found on the ground, in the shrubs and in the air. At Guadix, however, they are found almost exclusively on the ground (Table III), and most are ants. Overall, the breeding habitat provides more varied and more abundant prey than the wintering habitat, especially in spring. In relation to this different arthropod availability, the Black Redstart snatches half of its prey on the ground, and the remainder from the shrubs and in the air in Sierra Nevada (Table IV). Conversely, in Guadix, prey is taken almost exclusively from the ground. Likewise, substrate use differs more strongly between habitats than it does between time periods within each habitat (Table IV).

TABLE III

Seasonal variations in the mean (SD) number of arthropods captured per trap at ground level, on shrubs, and in the air, during the breeding season (Sierra Nevada) and in winter (Guadix).

	SIERRA NEVADA		GUADIX	
	Spring	Summer	Fall	Winter
Ground	116.1(123.6)	68.2(31.6)	57.9(47.9)	51.2(63.4)
Shrub	22.9(16.4)	15.5(11.4)	2.4(2.3)	0.0
Air	52.6(39.4)	15.3(12.3)	4.0(3.8)	0.1(0.2)

TABLE IV

The percentage of prey-capture attempts on each of the four substrates in the two habitats.

The order of statistical comparison is the same as in Table II. * = $p < 0.001$.

	Spring	Summer	OVERALL S. NEVADA	Fall	Winter	OVERALL GUADIX
Ground	44.9	48.1	46.8	96.7	97.8	97.3
Rock	2.6	1.9	2.1	0.0	0.0	0.0
Shrub	31.3	33.4	32.6	0.9	0.2	0.5
Air	21.2	16.6	18.3	2.4	2.0	2.2
N	614	1057	1673	457	554	1011
1/Σ pi ²	2.89	2.70	2.78	1.07	1.04	1.05
G-test	6.6, ns		909.2*		2.8, ns	

TABLE V

The percentages of substrate coverage, together with the percentages of substrate use.

The G-test compares the substrate availability with the substrate use in each period. * = $p < 0.001$.

SIERRA NEVADA

SUBSTRATE AVAILABILITY	SUBSTRATE USE		OVERALL
	Spring	Summer	
Ground	38.0	56.9	57.4
<i>J. communis</i>	41.2	25.8	18.4
<i>G. baetica</i>	7.8	13.8	20.6
<i>P. spinosum</i>	0.4	0.2	0.9
Rock	12.5	3.3	2.6
N	255	485	1366
G-test	22*		74*

GUADIX

SUBSTRATE AVAILABILITY	SUBSTRATE USE		OVERALL
	Fall	Winter	
Ground	71.4	99.1	99.5
<i>Artemisia sp.</i>	10.0	0.4	0.3
<i>R. sphaerocarpa</i>	12.8	0.2	0.1
<i>S. phloscae</i>	2.1	0.2	0.1
Stone	3.5	0.0	0.0
N	280	446	989
G-test	142*		230*

The Black Redstart selects bare ground for feeding to a greater extent than what actually corresponds to its coverage, especially in its wintering habitat, where the shrub layer is not used (Table V).

Some prey-capture techniques (e.g. perch-to-ground sallying) require the use of a perch for scanning the surroundings in search of prey. The Black Redstart uses rocks and shrubs as foraging perches in Sierra Nevada and Guadix (Table VI), although in both habitats it prefers rocks over shrubs.

Behavioural variability in the prey-capture techniques

The Black Redstart uses the perch-to-ground sallying and ground-foraging techniques preferentially in both its breeding and wintering habitats. This represents two clearly different searching strategies (perch-to-ground = passive searching, ground-foraging = active searching, Eckhardt, 1979). The between and within habitat comparison of both techniques can provide a more detailed analysis about the level of variability in hunting behaviour. In this comparison I will only consider perches used during successful prey captures.

TABLE VI

The percentages of substrate availability compared with the percentages of perch use.

The G-test compares the substrate availability with the substrate use in each period. * = p < 0.001.

SUBSTRATE AVAILABILITY		PERCH USE		OVERALL S. NEVADA
		Spring	Summer	
<i>J. communis</i>	62.5	15.8	12.1	14.1
<i>G. baetica</i>	11.9	20.5	30.2	25.4
<i>P. spinosum</i>	0.6	1.5	4.4	2.1
Rock	24.9	62.1	53.3	58.3
N	168	559	563	1152
G-test		139.2*	166*	170.8*

SUBSTRATE AVAILABILITY		PERCH USE		OVERALL GUADIX
		Fall	Winter	
<i>Artemisia sp.</i>	35.0	0.4	0.4	0.4
<i>R. sphaerocarpa</i>	45.0	58.0	30.6	45.4
<i>S. phloskae</i>	7.5	10.3	15.1	12.2
Rock	12.5	31.3	53.9	42.0
N	80	281	245	524
G-test		88.4*	107.2*	121*

a) *Perch-to-ground sallying*

In this technique, the bird uses a perch to look for prey on the ground. The Black Redstart uses higher perches in spring than in summer, and the same occurs in fall with respect to winter (see Fig. 1), although only in winter do significant statistical differences appear ($D = 0.185$, $p < 0.05$, Kolmogorov-Smirnov test). There is also a significant difference in the overall comparison between Guadix and Sierra Nevada ($D = 0.273$, $p < 0.001$). In Guadix, the perch-height distribution is bimodal, with a maximum in the interval 0-10 cm, corresponding to the stone substrate, and another less marked maximum between 60-150 cm, corresponding to the *R. sphaerocarpa* shrubs. In contrast the distribution of the perch-heights in Sierra Nevada is unimodal, with a maximum at 20-40 cm, which corresponds to the height of the majority of the scrubs and rocks (see Fig. 1).

The length of the stay on a successful perch is variable (range = 1-96 sec., see Fig. 2). The Black Redstart remains longer on the perches in Guadix than in Sierra Nevada ($D = 0.14$, $p < 0.05$), and significant differences are obvious

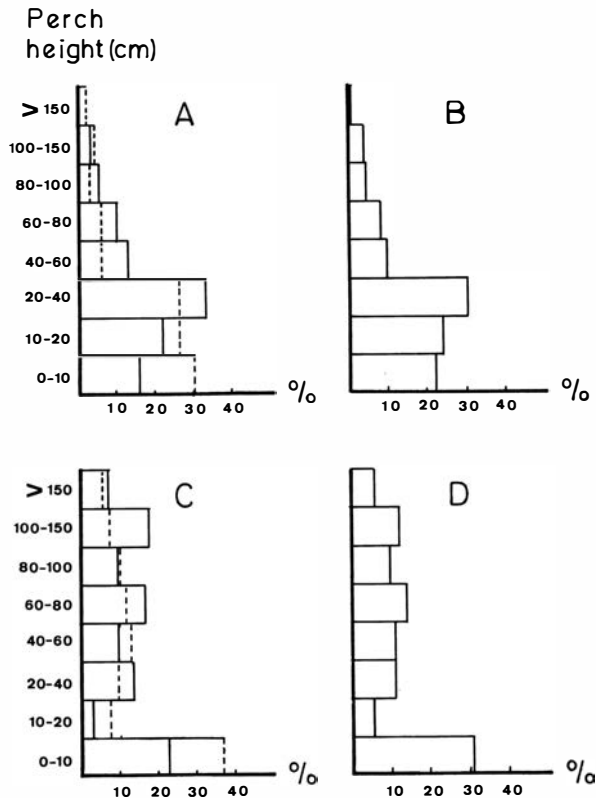


Figure 1. — Frequency distribution of the heights of foraging perches. A) spring (solid line, median = 30) and summer (dashed line, median = 18). B) Overall Sierra Nevada (median = 25). C) fall (solid line, median = 60) and winter (dashed line, median = 30). D) Overall Guadix (median = 45).

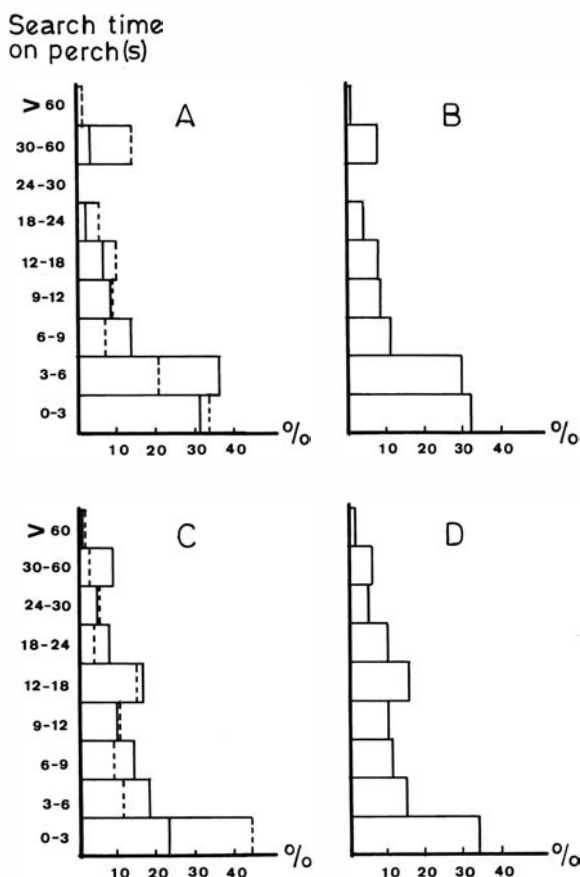


Figure 2. — Search time distribution for successful perches. A) spring (solid line, median = 5) and summer (dashed line, median = 6); B) Overall Sierra Nevada (median = 5); C) fall (solid line, median = 8), and winter (dashed line, median = 5); D) Overall Guadix (median = 7).

between spring and summer ($D = 0.193$, $p < 0.005$), and between fall and winter ($D = 0.21$, $p < 0.001$). It is noteworthy that the Black Redstart only needs three sec or less to make approximately 30 % of its prey-capture attempts. This would indicate that this species has an exceptionally short prey-detection time (Andersson, 1981).

There exists a very significant positive correlation between the length of stay and the height of the perch during the four periods (see Fig. 3 for statistical significance). Given the same perch height, there appears a shorter giving-up time in the spring and in the winter, compared to the fall and, above all, the summer. These differences could indicate temporal changes in prey selection and/or prey availability, especially in the breeding habitat (spring-summer).

The sallying distance was positively correlated both with the height of the perch (see Fig. 4 for statistical significance), and with the search time preceding sallies (spring : $r = 0.493$, $n = 54$; summer : $r = 0.323$, $n = 84$; fall : $r = 0.319$,

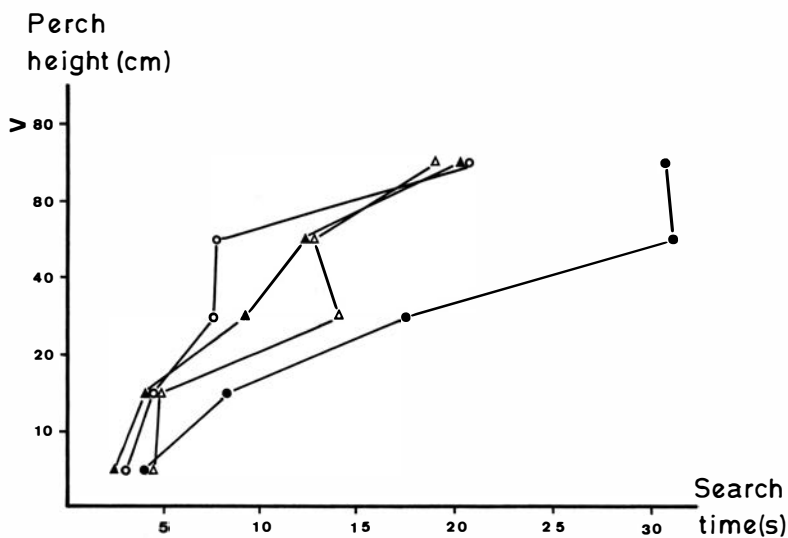


Figure 3. — Relationship between the height of the perch and the search time. Correlation values are : spring (open circles), $r = 0.596$, $df = 95$, $p < 0.001$; summer (filled circles), $r = 0.371$, $df = 71$, $p < 0.002$; fall (open triangles), $r = 0.286$, $df = 95$, $p < 0.005$; winter (filled triangles), $r = 0.323$, $df = 93$, $p < 0.001$.

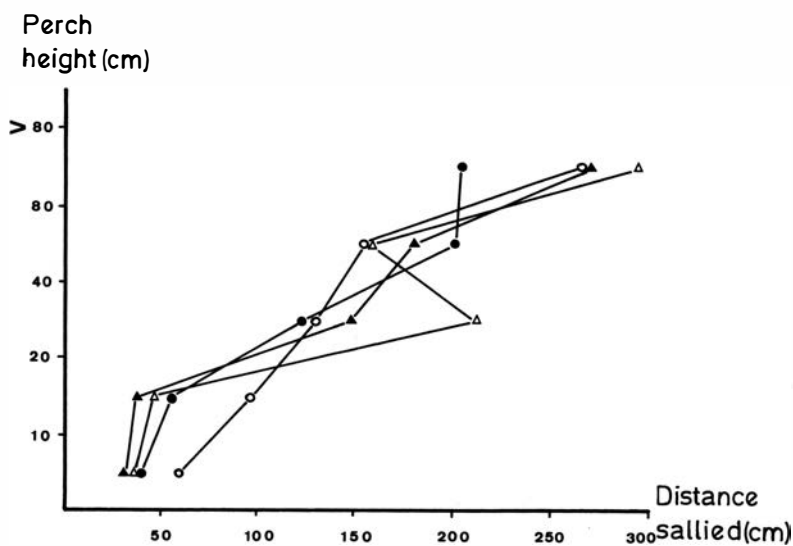


Figure 4. — Relationship between the height of a perch and the sallied distance. Correlation values are : spring (open circles), $r = 0.634$, $df = 83$, $p < 0.001$; summer (filled circles), $r = 0.894$, $df = 54$, $p < 0.001$; fall (open triangles), $r = 0.617$, $df = 98$, $p < 0.001$; winter (filled triangles), $r = 0.811$, $df = 93$, $p < 0.001$.

$n = 98$; winter : $r = 0.438$, $n = 93$, all correlations $p < 0.001$). This means that the higher the perch, the wider the scanning area, and that the bird looks for prey first on areas near its perch, before progressively focussing its attention further away (Moreno 1984).

The height of the perch and the length of the stay are two factors that may be related to prey-capture success ; this relationship enables the bird to choose the optimal height to achieve the greatest number of prey captures per unit of time. The capture probability (of each interval) has been calculated as the number of captures/second (Fig. 5) ; their values diminish as the height of the perch increases, although after 40 cm this decrease is very gradual.

Once having left, the Black Redstart usually changes to another perch, or initiates bouts of ground feeding. On few occasions, it returns to its previously used perch (the percentage values of return : Spring = 8.9 %, Summer = 2.6 %, Fall = 9.3 %, Winter = 7.4 %).

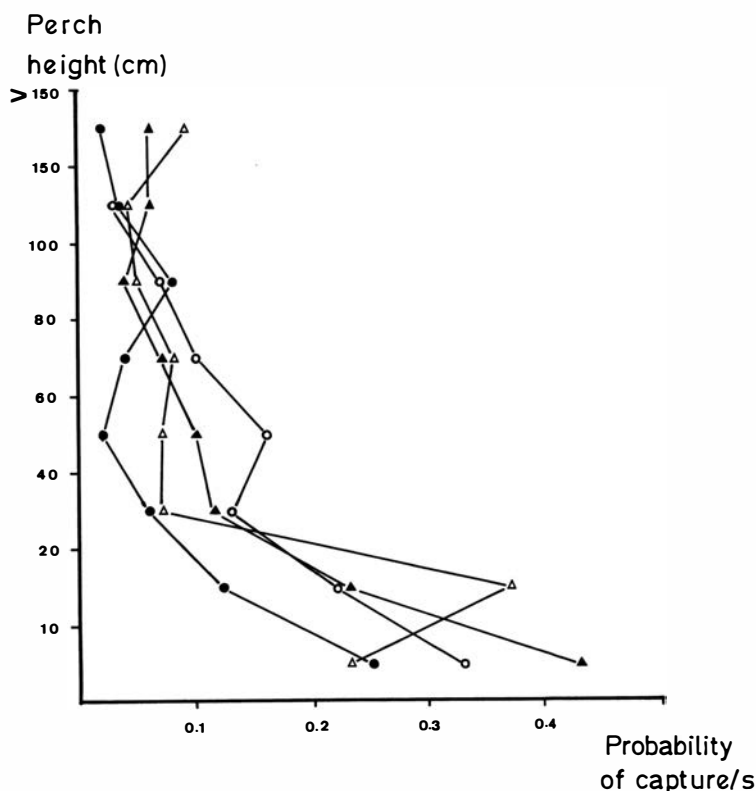


Figure 5. — Average probability of making a capture attempt per second with respect to the height of the perch. Open circles = spring, filled circles = summer, open triangles = fall, filled triangles = winter.

b) *Ground foraging*

A typical move by a Black Redstart foraging on the ground consists of a series of progressive jumps alternating with sudden stops (nearly 1 s or less) to look for prey (pause-travel search, Tye 1989). Some of these ground moves are interspersed with bouts of flying in the S. Nevada (Table VII), whereas pedal locomotion is used almost exclusively in Guadix. The flat muddy ground of the wintering habitat of our birds, with hardly any herbaceous vegetation, facilitates the pedal locomotion and the localization of prey. Probably for this reason, the Black Redstart covers a greater distance in Guadix than in Sierra Nevada ($Z = 2.13$, $p = 0.01$), although significant differences are found between spring and summer ($U = 390$, $p < 0.05$), but not between fall and winter ($U = 312.5$, $p > 0.05$). The hop rate is greater in Guadix than in Sierra Nevada ($Z = 2.91$, $p = 0.001$), and significant intrahabitat differences are not found (spring-summer, $U = 313$, $p > 0.05$; fall-winter, $Z = 1.01$, $p = 0.1$). Similar results are obtained when considering the capture rate: no significant intrahabitat differences are found (spring-summer, $U = 312.5$, $p > 0.05$; fall-winter, $Z = 1.03$, $p = 0.1$), whereas the Redstart captures, on the whole, more prey per time unit in Guadix than in the Sierra Nevada ($Z = 2.98$, $p = 0.001$).

During the winter, the Black Redstart takes 99 % of its prey on the ground, although in spring it frequently captures insects in the air and in the grasses by jumping and fluttering (Table VII).

The length of uninterrupted stays on the ground during the sequences of feeding is variable (range 2"-300", see Fig. 6). The Redstart remains on the ground for a longer time in Guadix than in Sierra Nevada ($D = 0.335$, $p < 0.001$), whatever the habitat (spring-summer, $D = 0.050$, n.s., fall-winter, $D = 0.110$, n.s.).

TABLE VII

Feeding behaviour on ground.

Figures corresponding to rate of travel, hop rate and attack rate are $\bar{X} \pm SD$, and figures corresponding to pedal locomotion, aerial locomotion and prey-capture on ground are percentages. The meaning of the parameters as in Table I.

	Spring	Summer	OVERALL S. NEVADA	Fall	Winter	OVERALL GUADIX
Pedal locomotion	75.7	73.8	74.5	96.2	96.6	95.5
Aerial locomotion	24.3	26.2	25.5	4.8	4.4	4.5
Rate of travel	8.8(5.6)	6.1(2.9)	6.9(4.1)	7.8(4.0)	10.2(3.4)	9.3(3.2)
Hop rate	14.4(5.7)	14.8(5.1)	14.7(5.1)	17.0(6.0)	20.9(6.9)	19.5(6.4)
Prey-capture rate	5.9(3.2)	5.5(3.3)	5.6(3.2)	9.9(5.4)	7.8(3.1)	8.6(3.8)
Captures on ground	63.6	91.5	82.6	99.1	99.0	99.0

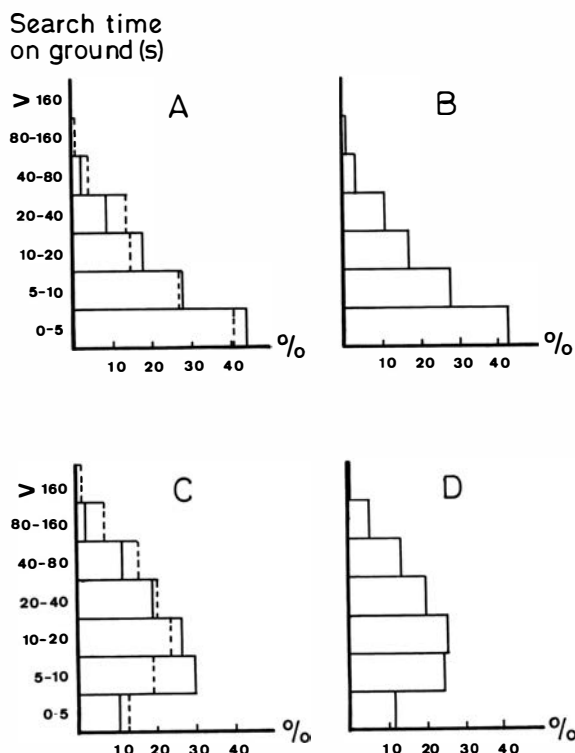


Figure 6. — Search time distribution on ground. A) spring (solid line, median = 6) and summer (dashed line, median = 7); B) Overall Sierra Nevada (median = 7); C) fall (solid line, median = 15) and winter (dashed line, median = 18); D) Overall Guadix (median = 16).

IV. — DISCUSSION

The Black Redstart's foraging behaviour is highly variable at different levels : 1) search modes ; 2) prey-capture repertoires ; 3) use of foraging microhabitats and perches ; 4) kinds of arthropods captured (from flying insects to burrowing species) ; and, 5) use of prey-capture techniques. What factors determine such a foraging variability ? The most parsimonious hypothesis is that both habitat and the distribution and abundance of arthropods determine the different ways in which the Black Redstart searches and captures prey in its breeding and wintering areas (see also Robinson and Holmes, 1982 ; Holmes and Recher, 1986 ; Holmes and Schultz, 1988). Furthermore, the unspecialised morphology (Zamora, 1988b), small size (16 g), and behavioural plasticity of the Black Redstart allow it to track the temporal variance of ecological factors, displaying a very flexible and opportunistic feeding behaviour throughout the seasonal cycle.

The differences in nature and structure of its breeding and wintering habitats bring about changes in the feeding behaviour of the Black Redstart, as seen in the use of feeding substrates (Holmes and Robinson, 1981, 1988 ; Pazskowski, 1982 ; Tye, 1988), as well as in the use of perches (Pinkowski, 1977 ; Brooke, 1981 ;

Moreno, 1984). For example, the stunted structure of the shrub layer in the high mountains allows the Black Redstart to use the upper surface of the scrub layer as its feeding and perching substrates. On the contrary, in its wintering habitat, where the scrub is much more open, it only uses stems as perches.

Overall, the temporal changes in the prey capture technique and use of microhabitats (Tables II and IV) are associated with changes in distribution and abundance of its arthropod prey (Table III). In this respect, the Black Redstart shows a more diverse repertoire of prey capture techniques in the Sierra Nevada, where it makes use of ground foraging and gleaning techniques, as well as aerial hawking, sally gleaning and perch-to-ground sallying. In Guadix, however, it becomes more specialised as a gleaner of ground prey (ground foraging and probe techniques); and it is also on this substrate that most of its prey (especially ants, Herrera 1978) are captured from perch. Our results therefore support the hypothesis that there is a negative relationship between predator mobility and prey mobility (Fitzpatrick, 1981; Huey and Pianka, 1981). Consequently, the repertoire of prey-capture techniques of the Redstart is geared towards the capture of very mobile prey (e.g. aerial hawking), as well as to the capture of immobile and/or buried prey (e.g. probe).

The temporal variation in prey abundance appears to determine the black Redstart's choice of prey from perch. For example, in summer and winter, the Redstart uses a lower perch than in spring and fall, which may indicate that during the former periods it concentrates its search on the ground. The Black Redstart remains on perch for shorter intervals of time than other species of similar ecology, like the Wheatear (*Oenanthe oenanthe*) (Moreno, 1984) and the Stonechat (*Saxicola torquata*) (Greig-Smith, 1984). This would imply a better visual capacity to detect prey, or a low prey selectivity.

The height of the perch determines the size of the scanning area for ground prey (Andersson, 1981). Given that the Black Redstart has a lower search time when using lower perches (Fig. 3), the bird probably searches for bigger and/or better quality prey when it sits on a higher perch to compensate for the cost associated with the increase in search time. The correlations found between the height of the perch and the length of the stay, and between the height and the prey-capture distance support this hypothesis (see also Fitzpatrick, 1981; Moreno, 1984; Greig-Smith, 1984).

The Redstart shows a low return percentage to the same perch after making a capture attempt, compared to the Wheatear (Moreno, 1984) and the Stonechat (Greig-Smith, 1984), as well as to other birds specialised in hunting insects in the air (Davies, 1977; Bibby and Green, 1980; Fitzpatrick, 1981). This is probably due to the «depression effect» (Charnov *et al.*, 1976) caused by the presence of the predator, which needs to be stronger in the case of a ground prey than for an aerial prey. The height of the perch also seems to condition the depression effect, given that the lower return percentages occur in summer and winter, when Black Redstart hunt from the lower perches (see also Moreno, 1984).

An important proportion of the variability of foraging behaviour of the Black Redstart may be due to changes in its energy needs in relation to prey availability. For example, a Black Redstart has to cover longer distances between and within patches in spring, although its attack rate does not increase (Table I). This behaviour could imply a greater prey selection during the breeding period, when prey availability is at a maximum. The opposite situation occurs in winter, when the Black Redstart shows its higher attack rate, even though the arthropod

availability is at a minimum. These results suggest that the bird becomes less selective in winter, taking smaller and/or less profitable prey (e.g. ants). The pause-travel search on ground allows it to maximise the area scanned per unit of time. For this reason, the Redstart prefers ground foraging in winter, when shorter days limit the searching period, and lower temperatures strongly decrease the number of moving arthropods.

In conclusion, the Redstart's switches between passive and active searching strategies obviously do not agree with the predictions of the « Syndrome Hypothesis ». The Black Redstart alternates short periods of searching on a perch (principally looking for aerial prey and/or mobile prey on ground) with brief pedal displacements (principally looking for slow-mobile and/or buried prey). This behaviour indicates a negative relationship between predator mobility and prey mobility (Huey and Pianka, 1981). The Black Redstart's search modes correspond to a relatively mobile bird with a move frequency of intermediate magnitude with respect to forest birds (see McLaughlin, 1989). Furthermore, the Redstart's rate of travel allows it to cover a large area in a short time, increasing the probability of prey encounters (i.e., maximizing the bird's search rate). In brief, the Black Redstart behaves as a generalist, open-habitat gleaner, or pause-travel predator (Tye, 1989), with a highly variable scanning area. It moves in the horizontal plane, unlike the typical foliage gleaners, which search in a small tridimensional volume of vegetation (e.g. Holmes and Robinson, 1981 ; Robinson and Holmes, 1984 ; Holmes and Recher, 1986).

SUMMARY

In this paper, I examine the search mode, prey-capture techniques and substrate use of the Black Redstart (*Phoenicurus ochruros*) in relation to habitat structure and the availability of arthropods in both its breeding and wintering habitats. The field work took place in two typical habitats of this species in southern Spain. Temporal variations in the prey-capture techniques and use of substrates were associated with the composition and structure of the habitats, and seasonal changes in the distribution and abundance of arthropods. The Black Redstart has a diverse repertoire of prey-capture techniques in its breeding habitat, while in its wintering quarters, it becomes more specialized, as a « ground gleaner ». The Redstart therefore switches between passive and active searching strategies, alternating short periods of searching on a perch with brief pedal moves. This behaviour increases the probability of encountering prey, indicating a negative relationship between predator mobility and prey mobility. In brief, the Black Redstart behaves as a generalist open-habitat gleaner, or pause-travel predator, with a highly variable scanning area.

RÉSUMÉ

Les modalités de recherche de la nourriture, les techniques de capture des proies et l'utilisation des substrats par le Rougequeue noir *Phoenicurus ochruros* ont été étudiées en rapport avec la structure du milieu et la disponibilité des

Arthropodes, à la fois dans son habitat de reproduction et dans ses quartiers d'hivernage. Cette étude a été faite dans deux milieux typiques de l'espèce, dans le sud de l'Espagne.

Les variations dans le temps des techniques de capture des proies et de l'utilisation des perchoirs varient avec la composition et la structure du milieu, ainsi qu'avec les changements saisonniers de distribution et d'abondance des Arthropodes. Le Rougequeue noir possède tout un répertoire de techniques de chasse dans son milieu de reproduction, alors qu'il devient un spécialiste (un « glaneur pédestre ») en hiver. Cette espèce passe donc, au cours de l'année, d'une « stratégie passive » à une « stratégie active », alternant de courtes périodes de recherche visuelle à partir d'un perchoir avec de brefs déplacements à terre. Un tel comportement augmente la probabilité de rencontre des Arthropodes, et indique qu'il y a une relation négative entre la mobilité du prédateur et celle de ses proies. Ce Rougequeue se comporte donc comme un glaneur généraliste de milieu ouvert, prédateur alternant pauses et mouvements, avec une zone de balayage visuel extrêmement variable.

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