

# DIET COMPOSITION AND PREY CHOICE OF THE SOUTHERN GREY SHRIKE *LANIUS MERIDIONALIS* L. IN SOUTH-EASTERN SPAIN: THE IMPORTANCE OF VERTEBRATES IN THE DIET

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**SUMMARY.**—*Diet composition and prey choice of the Southern grey shrike Lanius meridionalis L. in South-eastern Spain: the importance of vertebrates in the diet.*

**Aims:** The study of the diet and prey selection of the Southern grey shrike.

**Location:** Two shrubsteppes of South-eastern Spain.

**Methods:** The diet is determined by pellet analysis, and then compared with samples of prey availability recorded by means of pitfall traps, on a monthly basis during an annual cycle.

**Results:** The Southern grey shrike consumes several beetle types, grasshoppers, and, during the breeding period, lizards. Birds and small mammals are captured incidentally. It consistently rejects prey smaller than 10 mm long, and prey are larger during the breeding period and summer. Compared with other populations of Southern grey shrike and also with Northern grey shrike, the population studied here shows a greater importance of lizards in the diet. Birds and mammals, which are progressively more frequent in diet as latitude increases, both in breeding and wintering periods, are here at low frequency.

**Conclusions:** The diet of the Southern grey shrike in South Spain combines arthropods (mainly between 10 and 30 mm in length) and lizards. The changes in the taxonomic groups captured along an annual cycle and their sizes suggest that, apart of the weak limits of prey size described, the Southern grey shrike is quite opportunistic when feeding, and captures any prey of the adequate size available, regardless of their taxonomy. This also corresponds with the changes in diet showed along the European continent by both the Southern and the Northern grey shrike.

*Key words:* food availability, pellet analysis, pitfall traps, prey size, prey selection.

**RESUMEN.**—*Composición de la dieta y selección de presa en el alcaudón real Lanius meridionalis L. en el Sureste de España: la importancia de los vertebrados en la dieta.*

**Objetivos:** Describir la dieta y analizar la selección de presa del alcaudón real.

**Localidad:** Dos estepas arbustivas del Sureste de España.

**Métodos:** Análisis de egagrópilas y comparación de la dieta con la disponibilidad de artrópodos en una de las zonas, evaluada mediante trampas de caída, ambos datos recogidos mensualmente durante un ciclo anual.

**Resultados:** El alcaudón real basa su dieta en diversos tipos de escarabajos, saltamontes y, en la época de reproducción, en lagartijas. Aves y mamíferos sólo son capturados ocasionalmente. En cuanto al tamaño de presa, rechaza las presas pequeñas (menos de 10 mm de longitud). Las presas alcanzan sus mayores tamaños durante la reproducción y el verano. En comparación con otras poblaciones de alcaudón real y de alcaudón norteño, este estudio muestra una gran importancia de los reptiles y una reducida proporción de aves y mamíferos, que son más importantes cuanto más al norte se efectúa el análisis.

**Conclusiones:** El alcaudón real en el sur de la península Ibérica combina en su dieta artrópodos, generalmente de entre 10 y 30 mm de longitud, y lacértidos. La variación estacional de los grupos taxonó-

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micos consumidos y sus tamaños sugieren que, aparte de estos límites bastante flexibles de tamaño, el alcaudón es bastante oportunista y consume en cada lugar y en cada momento los grupos taxonómicos de tamaño adecuado que están presentes. Esto también se corresponde con la variación en la dieta que alcaudón real y norteño muestran a lo largo del continente europeo.

*Palabras clave:* análisis de egagrópilas, disponibilidad de alimento, tamaño de presa, trampas de caída.

## INTRODUCTION

The Southern grey shrike *Lanius meridionalis* has been considered until recently as a subspecies of the Northern grey shrike *L. excubitor* (Isenmann and Bouchet, 1993; Isenmann and Lefranc, 1994). Apart of morphological and biochemical characteristics (Lefranc and Worfolk, 1997; Hernández *et al.*, 2004), some ecological features, such as habitat and diet, have been suggested to differentiate the two species (Schön, 1998; Hernández, 2000). In Europe, the Northern grey shrike is distributed in cold and wet climates of the north, while the Southern great shrike prefers dry and warm areas of the Mediterranean, as well as North Africa and the Near and Middle East (Lefranc and Worfolk, 1997). In agreement with this distribution and habitat selection, it has been suggested that the Northern grey shrike preys mainly on warm-blooded animals (birds and mammals) in the cold habitats that inhabits, while the Southern grey shrike preys on cold-blooded ones (Schön, 1998; Hernández, 2000; Lepley *et al.*, 2004), as an adaptation to its more arid distribution area. However, there is doubt whether these contrasts in diet are the effects of the different preferences or hunting strategies by the two species, or simply the consequence of varying prey availability in the different distribution areas (Lepley *et al.*, 2004).

A thorough analysis of diet of both species in a wide gradient of habitats is needed in order to resolve these doubts; however, this analysis is still lacking. Furthermore, while the diet of the Northern grey shrike is well known in many parts of its distribution (Mester, 1965; Grönlund *et al.*, 1970; Haensel and Heuer, 1970, 1974; Huhtala *et al.*, 1977; Bassin *et al.*,

1981-83; Jentzsch and Otto, 1988; Ruppe and Materna, 1990; Grimm and Haensel, 1991; Karlsson, 2002; Hromada *et al.*, 2003), this is not so with the Southern grey shrike, for which only the works of Hernández (1993, 1995a, 1995b, 1999; Hernández *et al.*, 1993) in Northern Spain, Lepley *et al.* (2004) in La Crau (France) and Padilla *et al.* (2005) in Canary Islands provide detailed dietary information, although there is also some scattered data in Southern Spain (Soler *et al.*, 1983) and Israel (Yosef *et al.*, 1991; Budden and Wright, 2000).

In this context, the aim of this work is threefold. First, I provide the description of the diet on the Southern grey shrike in one of its typical habitats, namely two arid shrubsteppes, in south-eastern Spain. Second, I compare its diet with prey availability, in order to understand the processes that determine its prey selection. Finally, I review the data available until now for the diet both the Southern and the Northern grey shrikes along a latitudinal gradient across Europe, and explore how the variations in diet fit with the above-mentioned assumptions, in order to elucidate whether the dietary differences between the Southern and the Northern grey shrikes are characteristic of the species or the effect of different prey availability.

## MATERIAL AND METHODS

### *Study area*

The general study area is the Hoya de Guadix-Baza, a Neogene basin surrounded by high mountains (1700 - 3000 m asl) some 700 - 1100 m asl. The climate is Mediterranean continental, with cold winters and warm, dry summers (Castillo-

Requena, 1990). Annual rainfall oscillates between 300 - 350 mm, but during the study period, in 1990 and 1991, the respective annual rainfall was 305 and 281 mm in Baza and 244 and 263 mm in Guadix. Field work was performed in two seasonal watercourses (called *ramblas*), usually dry all year, with floods only during strong storms in spring and autumn. Briefly, the two study sites were: the Barranco del Espartal (37° 32' N, 2° 41' W, 750 m a.s.l., hereafter Baza), a *rambla* in a badlands landscape with a substrate of silt with gypsum sediments; and the Rambla del Grao (37° 22' N, 3° 8' W, 950 m a.s.l., hereafter Grao) with clay soils. The distance between the two zones is around 50 km. The vegetation is shrubby and sparse (33 % shrub cover in Baza, 17 % in Grao), bare ground reaching 46 % cover in Baza and 60 % in Grao. The vegetation is scattered and low (mean around 80 cm), mainly shrubs of *Salsola* spp., *Artemisia* spp. and *Retama sphaerocarpa*, and scant grasses and forbs. In both cases, work was conducted in the lower part of the *rambla* and the surroundings, covering an area of ca. 3 km<sup>2</sup> each.

### General methods

The dietary study was based on pellet analysis, collections made biweekly between November 1990 and October 1991. Although the Southern grey shrike usually impales preys and stores them in caches for several days (see Yosef and Pinshow, 1989), this behaviour is uncommon in both study sites, probably due to the lack (Baza) and scarcity (Grao) of thorny shrubs. Only five impalings in Baza and four in Grao were recorded during 12 months of field work. Because of this, the impaling data are not included in the numerical analysis of the diet. The months with the largest sample size were the breeding period, because adults showed restricted activity around the nest, and pellets were easily located. Baza had a more continuous sampling than in Grao. In Baza, perches are mainly signposts marking hunting

preserves, usually situated at good vantage points. In Grao, perches were *Pinus* trees and *Retama* shrubs, more dispersed and usually higher, for which intact pellets were scarce and more difficult to find. For this reason, Grao data corresponds only to six of the months of study, while in Baza data are lacking for January. Perches were also eventually used by black wheatear (*Oenanthe leucura*) and black-eared wheatear (*Oenanthe hispanica*), but their remains were easily identifiable (Hódar 1995, 1998a), while woodchat shrike (*Lanius senator*) in general used different perches than Southern grey shrike.

Pellets were collected by surveying the usual hunting perches of birds, as well as roosting shrubs. The ground near perches was cleaned after each visit. Only complete pellets were collected; any damaged, broken or deteriorated pellets were discarded. The samples were not divided according to territories, because the exact limits of the hunting range of a pair were difficult to determine, especially during winter, and the animals were not individually recognizable. For the sampling effort to be equal between pairs, sampling perches were distributed as evenly as possible in the study area, and the number of pellets per perch and month was limited to up to five. Since sampling was always made in the same area and all pellets were collected, it was assumed that every bird living in the area had the same probability of being sampled. The mean density of shrikes during study period (estimated by variable line-distance transect; Burnham *et al.*, 1980; Verner, 1985) was around 0.15 ind/10 ha in Baza and 0.18 ind/10 ha in Grao, with wide fluctuation year-round in both cases (Hódar, 1996b). During the breeding period, at least three pairs occupied each zone.

Pellets were separated dry and examined with a binocular microscope (10 - 40x). Preys were identified with the aid of a reference collection of arthropods collected in the study areas. Estimation of prey length and biomass was made with a series of allometric equa-

tions formulated with arthropods from study areas (Hódar, 1996a, 1997). For vertebrate prey, length was estimated disregarding the tail, and biomass was also considered in dry weight. For mammals and birds, the mean length and weight were assigned from captures in the study area (Hódar, 1993); for lizards, length and weight were estimated from the length of the dentary bone (the most usual and measurable remains in pellets), by means of the equations  $W = 0.988 \times M^{3.404}$ , ( $n = 7$ ,  $R^2 = 0.958$ ,  $P < 0.001$ ;  $M$  = mandible length in mm,  $W$  = lizard dry weight, in mg) and  $L = 7.61 \times M - 3.51$  ( $n = 15$ ,  $R^2 = 0.971$ ,  $P < 0.001$ ;  $L$  = snout-vent length, both  $L$  and  $M$  in mm).

Dietary data were computed on a monthly basis, both numerical 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). Non-parametric tests were applied because of the heteroscedasticity and non-normal distribution of prey sizes (Zar, 1996). Comparisons of dietary compositions were made with  $G$  tests, whereas prey sizes were compared with the Mann-Whitney and Kruskal-Wallis tests.

Arthropod availability was estimated in Baza using pitfall traps (Cooper and Whitmore, 1990). A total of 36 pitfalls were placed biweekly (sampling period: 48 h) throughout the study period, distributed throughout all the microhabitats of the study area (Sánchez-Piñero, 1994). Traps were distributed in three groups, sparse along the study areas; every group was composed of six pairs of pitfalls (distance within pair 2 m, distance between pairs 5-10 m). Selectivity was quantified using the  $W_i$  Savage index, and significance of selection evaluated by  $\chi^2$  test (Manly *et al.*, 1993), with a *posteriori* correction of significance by sequential Bonferroni procedure (Rice, 1989). Pitfall traps did not capture vertebrates, and because of this these groups were not included in the selectivity analysis. For the calculations of  $W_i$ , arthropods recorded in

both diet and availability were classified by taxonomic groups and size classes (4 mm each). Since pitfalls do not reflect arthropod availability in the same way that the shrike does (Rosenberg and Cooper, 1990; Wolda, 1990), the availability data was handled in two ways to approximate both approaches. First, all types of small prey that shrike never eat (Collembola, Acarina, Thysanoptera and similars) were removed, as well as other arthropods less than 2 mm length, because the minimum prey length recorded for shrike in the two zones was 3 mm. Secondly, a relative frequency of 0.01 % was arbitrarily assigned to all groups consumed by shrike in a specific month but not recorded in pitfalls in the same month. Because birds cannot prey upon groups that are not present, this information was required to calculate selectivity. This correction was applied to 13 out of 130 cases for prey taxa and 11 out of 87 cases for prey size.

For comparisons with other studies showing the diet on a seasonal basis, breeding period was considered as April, May and June, and winter as December, January, February and March. The use of these two seasons for comparison was chosen because most of the available works do not express the data on a monthly basis, but rather restrict their data to breeding and/or winter.

## RESULTS

A total of 329 pellets were analysed (203 from Baza and 126 from Grao), resulting in 2100 identified prey (1403 and 697, respectively). Arthropods represent 90.5 % of captures, but vertebrates account for 66.3 % of the prey biomass, despite they reach a scant 9.5 % of captures.

### *Prey composition*

Prey groups showed marked variations throughout the year (Baza:  $G = 1265.05$ ,  $P <$

0.001, Grao:  $G = 505.32$ ,  $P < 0.001$ ; Tables 1 and 2). In Baza, in early spring, the main preys were Scarabeidae, due mainly to *Rhizotrogus toletanus*, a beetle that emerges explosively between March and April. Later in spring, *Rhizotrogus* is replaced by *Amphimallon* sp. and several species of dung beetles. During breeding period, lizards were the basic prey both in frequency and biomass. Summer showed a progressive increase in Orthoptera, which continue as major part of the diet until winter. In autumn, when the rain started, Tenebrionidae and Curculionidae appeared (Table 1). In Grao, the monthly pattern was similar, but *Rhizotrogus* was absent, and therefore the spring diet was composed mainly of lizards and Tenebrionidae (Table 2). Thus, there was a good match between the appearance of different kinds of prey and their capture by the shrike.

Predation upon birds and small mammals is restricted in Baza to winter (except a capture in August), whereas in Grao such predation was more common throughout the year. All mammals in Baza were shrews *Suncus etruscus*, but in Grao mice *Mus* sp. and *Apodemus sylvaticus*. Birds were the Greenfinch *Carduelis chloris*, Sardinian Warbler *Sylvia melanocephala* and Alaudidae-Motacillidae unidentified; in the Baza zone there one capture record was a Stonechat *Saxicola torquata* outside the study area during study period (R. Zamora, pers. com.). Lizards found in pellets were usually impossible to distinguish to the species level, but the most common species in both zones were *Psammodromus algirus*, *P. hispanicus* and *Acanthodactylus erythrurus*.

Both zones showed significant differences in diet composition ( $G = 441.34$ ,  $P < 0.001$ ).

#### Prey size and biomass

Prey size was smallest in winter and early spring, increasing during the breeding period and reaching peak values in late summer and autumn. In Baza, variations in prey size were

wide (Kruskal-Wallis test:  $H = 229.25$ ,  $df = 10$ ,  $P < 0.001$ ), the mean monthly minimum being half the mean monthly maximum (Table 1), whereas in Grao the prey length proved more stable (Kruskal-Wallis test:  $H = 2.82$ ,  $df = 5$ ,  $P > 0.05$ ; Table 2), and consistently larger than in Baza. Both zones showed significant differences in prey length (Mann-Whitney test:  $Z = 7.36$ ,  $P < 0.001$ ) and biomass ( $Z = 3.00$ ,  $P = 0.0027$ ).

Monthly amounts of biomass in diet showed a different view than offered by frequency data. In both zones, arthropods (mainly Coleoptera) predominated in the number of captures (up to 75 % of the prey in April; Tables 1 and 2), but vertebrates accounted for more than 40 % of the biomass in 8 out of 11 months in Baza, and 5 out of 6 in Grao, coinciding with the winter (birds and mammals) and the breeding period (lizards). Apart of the vertebrates, Orthoptera and Coleoptera were the other main contributors in biomass throughout the year in both zones; only occasionally Arachnida, Araneae or Myriapoda reach up to 5 % in biomass.

#### Relationship diet-availability

From the taxonomic standpoint, only Formicidae were significantly rejected as prey by the Southern grey shrike; the rest of the groups were usually captured above their availability, and at times not captured (Table 3). They significance of Scarabeidae in spring-summer was noteworthy (due to *Rhizotrogus* and *Amphimallon*), as was Carabidae during summer, and Orthoptera and Heteroptera during July and August, the driest months. In autumn, Orthoptera and Tenebrionidae remained significant, and during winter Tenebrionidae was replaced by Curculionidae.

The analysis of prey-size selectivity matched quite well with the selection of taxonomic groups. When prey size was below 10 mm (mainly Formicidae) prey were almost

TABLE 1

Taxonomic composition of the diet of the Southern grey shrike in the Barranco del Espartal, Baza (Granada, SE Spain). Data are offered as percentages of numerical frequency (%F) and biomass (%B). Prey size (in mm) is given as mean  $\pm$  standard error.

[Composición taxonómica de la dieta del alcaudón real en el Barranco del Espartal, Baza (Granada, SE de España), expresada como porcentajes de frecuencia (%F) y biomasa (%B). El tamaño de presa se ofrece (en mm) como media  $\pm$  error estándar.]

Taxa	Month		February		March		April		May		June		July		August		September		October		November		December		
	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	
Araneae	0	0	0.8	1.4	1.8	2.5	0	0	0	0	0	0	3.3	1.2	0	0	3.2	12.6	4.1	4.5	5.8	3.5	1.0	0.5	
Arachnida	0	0	0	0	0	0	2.5	0.7	15.8	7.0	10.0	4.1	2.9	0.4	0	0	0	0	0	0	0	0	0	0	
Myriapoda	8.2	6.4	2.2	5.2	0.7	1.4	0	0	0	0	0	0	0	0	1.6	0.2	1.4	0.2	6.7	7.6	3.9	3.7			
Orthoptera	1.4	1.2	5.3	11.8	1.8	2.9	5.1	4.2	5.3	9.8	16.7	21.7	45.7	23.1	23.8	36.7	13.0	28.6	26	42.3	24.3	28.9			
Heteroptera	1.4	0.3	0	0	0	0	1.9	0.3	5.3	1.6	13.3	4.2	2.9	0.3	0	0	0.7	0.3	0	0	0	0	0	0	
Carabidae	4.1	0.8	1.9	1.4	1.1	0.3	12.0	6.3	5.3	3.9	13.3	4.2	4.3	0.5	1.6	3.0	6.8	10.3	5.8	7.3	1.9	1.7			
Tenebrionidae	0	0	2.2	3.9	10.5	8.8	9.5	5.7	15.8	16.0	0	0	4.3	1.5	34.9	33.3	27.4	30.6	25.0	14.9	2.9	1.4			
Scarabeidae	0	0	42.7	16.5	56.5	17.1	11.4	3.1	10.5	3.8	0	0	1.4	0.4	0	0	5.5	1.6	1.9	0.4	1.0	1.2			
Curculionidae	41.1	8.3	14.1	4	6.2	1.4	5.1	1.0	0	0	3.3	1.9	7.1	1.4	3.2	1.6	4.8	2.1	8.7	2	22.3	4.7			
Coleoptera oth.	1.4	0.3	1.7	1.6	0.7	0.3	5.7	4.7	21.1	15.6	16.7	16.5	4.3	1.2	3.2	1.6	23.3	14.4	3.8	1	1.9	0.2			
Formicidae	13.7	0.2	14.7	0.3	1.8	0.1	10.8	0.1	0	0	10.0	0.4	5.7	0.1	23.8	1.6	8.2	0.5	2.9	0.1	24.3	0.6			
Hymenoptera	20.5	2.9	9.4	3.0	8.3	2.6	10.8	1.7	0	0	3.3	0.6	5.7	0.5	0	0	0.7	0.2	1.9	0.7	6.8	1.1			
Insecta oth.	5.5	0.9	3.6	1.0	7.6	1.8	8.9	1.3	10.5	2.1	0	0	2.8	0.3	1.6	0.2	2.7	0.5	7.7	1.9	8.8	1.3			
Reptilia	0	0	0.6	1.0	2.2	11.9	16.5	71.0	40.2	10.0	45.2	11.4	28.5	3.2	9.1	1.4	6.3	3.8	18.4	0	0				
Aves	1.4	73.0	0.6	47.0	0.7	49.2	0	0	0	0	0	0	1.4	41.8	0	0	0	0	0	0	0	0	1.0	54.8	
Mammalia	1.4	5.6	0.3	1.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
N° pellets	10	36	36	30	30	33	33	33	3	3	6	6	11	11	17	17	17	17	18	18	18	12			
Prey identified	73	361	361	276	276	158	158	158	19	19	30	30	70	70	63	63	63	63	146	104	104	103			
Prey measured	61	303	303	233	233	131	131	131	14	14	19	19	58	58	59	59	59	59	135	92	92	95			
Prey length	13.2 $\pm$ 1.4	14.2 $\pm$ 0.5	13.1 $\pm$ 0.5	19.9 $\pm$ 1.2	17.8 $\pm$ 1.5	16.8 $\pm$ 1.7	26.6 $\pm$ 2.1	20.2 $\pm$ 1.3	19.8 $\pm$ 0.7	21.0 $\pm$ 1.1	17.0 $\pm$ 1.2														



TABLE 2

Taxonomic composition of the diet of the Southern grey shrike in the Rambla del Grao (Granada, SE Spain). Data are offered as percentages of numerical frequency (% F) and biomass (% B). Prey size (in mm) is given as mean  $\pm$  standard error.

[Composición taxonómica de la dieta del alcaudón real en la Rambla del Grao (Granada, SE de España), expresada como porcentajes de frecuencia (% F) y biomasa (% B). El tamaño de presa se ofrece (en mm) como media  $\pm$  error estándar.]

Taxa	Month		February		March		April		May		July		November	
	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B	%F	%B
Araneae	2.2	3.2	2.6	7.4	1.7	0.5	0.6	0.3	0	0	0	0	0	0
Arachnida	0	0	3.9	0.1	0	0	6.4	0.1	4.0	2.4	0	0	0	0
Myriapoda	0	0	1.3	4.0	0	0	0	0	1.0	0.1	0	0	0	0
Orthoptera	8.7	7.9	6.6	14.0	8.3	7.0	1.8	0.8	36.0	25.6	27.9	57.1		
Heteroptera	0	0	5.3	1.3	1.7	0.1	1.8	0.3	0	0	0	0	0	0
Carabidae	0	0	2.6	0.7	3.9	0.8	1.8	0.4	0	0	7.0	23.9		
Tenebrionidae	32.6	15.1	11.8	8.4	32.8	4.4	19.9	3.1	0	0	0	0	0	0
Scarabeidae	0	0	1.3	1.0	6.1	0.8	0.6	0.7	0	0	2.3	1.4		
Curculionidae	18.5	4.3	17.1	8.2	3.9	0.4	1.2	0.2	8.0	2.0	2.3	1.1		
Coleoptera oth.	4.3	0.8	1.3	1.0	4.4	0.3	19.3	1.6	6.0	0.6	9.3	7.4		
Formicidae	12.0	0.3	5.3	0.3	3.3	0.1	9.4	0.1	28.0	0.5	41.9	6.1		
Hymenoptera	4.3	0.3	23.7	8.9	3.9	0.1	5.8	0.3	4.0	0.4	4.7	1.7		
Insecta oth.	3.3	0.3	5.2	1.8	2.8	0.2	1.8	0.1	0	0	4.7	1.4		
Reptilia	13.0	13.3	11.8	43.1	23.9	21.1	28.1	52.8	13.0	68.5	0	0		
Aves	1.1	54.7	0	0	1.1	23.8	0	0	0	0	0	0		
Mammalia	0	0	0	0	2.2	40.5	1.8	40.1	0	0	0	0		
Nº pellets	22		11		36		34		18		5			
Prey identified	92		76		180		206		100		43			
Prey measured	84		70		163		174		89		38			
Prey length	19.2 $\pm$ 1.3		17.7 $\pm$ 1.2		24.4 $\pm$ 1.5		22.6 $\pm$ 1.3		22.2 $\pm$ 1.6		19.4 $\pm$ 1.3			

always captured below their availability ( $W_i$  values below 1), while most of the sizes above 10 mm were positively selected ( $W_i$  values above 1), although the selection was not always significant. Prey between 10-14 mm were positively selected year-round, while the biggest prey, above 22 mm, were selected mainly during the breeding period and the summer months (corresponding to the period where shrikes were feeding either chicks at the nest or fledglings), and during autumn (when grasshoppers reach the end of their development).

## DISCUSSION

The main features of the Southern grey shrike diet in the arid zones of south-eastern Spain agree in general with previous studies on the species. In the present study, arthropods, mainly beetles and grasshoppers, proved to be the staple food for most part of the year. There was a good match between the emergence of different groups of arthropods, especially those with explosive phenology, and their frequency in the shrike's diet. In any case, the results of the selectivity analysis suggest

TABLE 3

Selectivity values ( $W_i$  Savage's index) for the different prey types and prey-size classes (in mm) found in the diet of the Southern grey shrike in the Barranco del Espartal, Baza (Granada, SE Spain). Figures in bold are significant after a correction with *a posteriori* sequential Bonferroni procedure.

[Valores de selectividad ( $W_i$ , índice de Savage) para los diferentes tipos de presa e intervalos de tamaños encontrados en la dieta del alcaudón real en el Barranco del Espartal, Baza (Granada, SE España). Las cifras en negrita son significativas tras una corrección *a posteriori* mediante el procedimiento secuencial de Bonferroni.]

Prey groups	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Araneae	0.0	0.2	0.3	0.0	0.0	1.7	0.0	1.4	1.1	2.8	0.2
Arachnida		0.0		9.9	<b>41.3</b>	<b>49.8</b>	12.8		0.0		
Myriapoda	11.0	3.6	2.1		0.0			7.2	3.8	3.3	4.2
Orthoptera	5.5	8.6	0.8	2.6	5.3	<b>15.1</b>	<b>102.4</b>	<b>27.0</b>	<b>36.3</b>	<b>50.8</b>	<b>26.5</b>
Heteroptera	1.4		0.0	3.7	11.5	<b>66.4</b>	<b>51.2</b>	0.0	1.9	0.0	
Carabidae	4.1	3.2	3.2	<b>31.2</b>	<b>68.8</b>	<b>44.2</b>	<b>76.8</b>	7.2	3.2	0.9	2.1
Tenebrionidae		3.6	0.6	1.6	<b>6.9</b>	0.0	3.3	<b>7.2</b>	<b>12.7</b>	<b>24.4</b>	3.2
Scarabeidae		<b>69.6</b>	<b>167.6</b>	<b>88.8</b>	<b>137.5</b>		25.6	0.0	15.3	3.8	1.1
Curculionidae	<b>20.6</b>	4.6	1.7	7.9	0.0	<b>33.2</b>	<b>64.0</b>	1.8	1.9	4.2	<b>12.2</b>
Coleoptera ot.	0.3	0.2	0.1	0.8	<b>7.9</b>	<b>10.4</b>	12.8	0.6	4.3	0.2	0.2
Formicidae	0.4	<b>0.2</b>	0.1	0.3	<b>0.0</b>	<b>0.1</b>	<b>0.1</b>	<b>0.3</b>	<b>0.1</b>	0.1	0.6
Hymenoptera	3.9	<b>15.4</b>	4.9	4.7	0.0	2.0	9.3	0.0	0.6	0.5	7.4
Insecta oth.	0.1	0.2	0.3	0.5	1.6	0.0	1.8	0.3	0.1	0.4	0.2
<b>Prey sizes</b>											
2.1-6	<b>0.2</b>	<b>0.1</b>	<b>0.1</b>	<b>0.1</b>	<b>0.0</b>	0.0	<b>0.1</b>	0.1	<b>0.0</b>	<b>0.1</b>	<b>0.1</b>
6.1-10	0.3	0.7	0.9	0.4	0.0	0.3	0.3	0.1	0.5	0.4	3.8
10.1-14	<b>11.1</b>	<b>26.2</b>	<b>25.5</b>	<b>7.7</b>	<b>12.3</b>	<b>36.2</b>	<b>19.5</b>	<b>10.9</b>	1.9	4.3	<b>12.6</b>
14.1-18	6.6	4.1	0.6	5.4	<b>19.1</b>	2.9	<b>24.5</b>	<b>9.3</b>	<b>14.1</b>	<b>51.1</b>	11.5
18.1-22	0.0	13.5	2.4	2.8	5.0	<b>10.0</b>	5.7	1.4	5.7	4.1	1.1
22.1-26	0.0	1.1	5.0	<b>38.1</b>	<b>179.8</b>	<b>24.9</b>	<b>41.7</b>	<b>18.9</b>	<b>37.2</b>	8.9	1.1
26.1-30	6.6	3.8	1.2	5.9	0.0	0.0	<b>109.3</b>	<b>18.9</b>	10.3	<b>20.4</b>	10.3
≥ 30.1	0.0	7.0	0.0	17.6	0.0		<b>437.4</b>	<b>60.6</b>	16.5	<b>28.6</b>	<b>16.1</b>

that, regardless of their taxonomic group, the prey captured by the shrike measured between 10 - 30 mm in length. In the study area, this usually coincides with beetles and grasshoppers for most of the year, the single exception being lizards during the breeding period, probably the staple food for feeding the chicks. Very abundant possible prey such as worker ants, heavily consumed by other birds with similar hunting patterns in the area, either during summer (black and black-eared wheatears;

Hódar, 1995, 1998a) or winter (black redstart *Phoenicurus ochruros*; Hódar 1998b), are systematically rejected by the shrike. For birds inhabiting arid zones, ants are usually available and abundant, in Baza reaching 58.9 % of total arthropod individuals caught in pitfall traps, and 71.9 % in Grao (Sánchez-Piñero, 1994; Sánchez-Piñero and Gómez, 1995). However, ants do not seem to represent an adequate food source for the shrike, and only when swarms of winged ants fly in autumn do



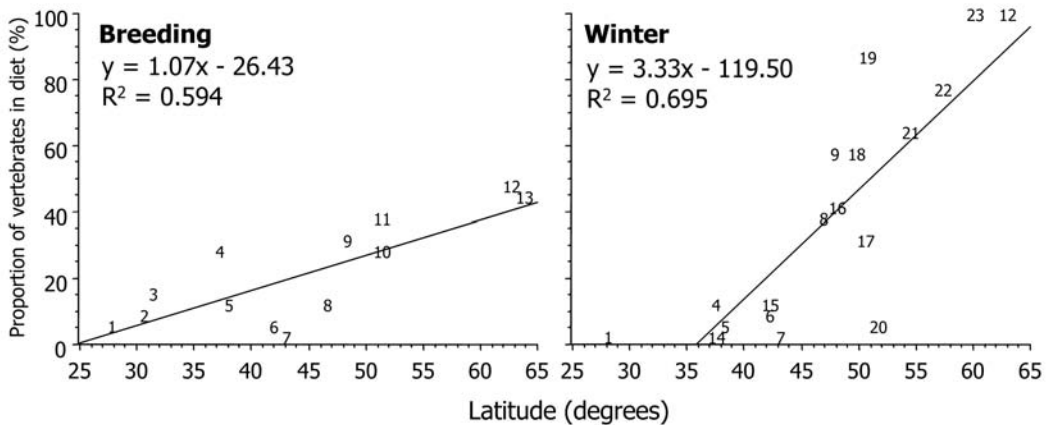


FIG. 1.—Relationship between the proportion of vertebrates in the diet of the Northern and Southern grey shrike in Europe, and the latitude at which the study was made. The results are separated for those studies performed during the breeding and the winter seasons. When a study has data in both seasons, the code is the same in both panels. 1: Padilla *et al.* 2005; 2: Yosef *et al.*, 1991; 3: Budden and Wright, 2000; 4: This study, Grao; 5: This study, Baza; 6: Hernández, 1993; 7: Lepley *et al.* 2004; 8: Bassin *et al.*, 1981–1983; 9: Bohác, 1964; 10: Grimm and Haensel, 1991; 11: Ruppe and Materna, 1990; 12: Grönlund *et al.*, 1991; 13: Huhtala *et al.* 1977; 14: Soler *et al.*, 1983; 15: Nikolov *et al.*, 2004; 16: Bayer, 1950; 17: Bocca, 1999; 18: Oeser, 1974; 19: Jentzsch and Otto, 1988; 20: Haensel and Heuer, 1970; 21: Knysh *et al.*, 1991; 22: Olsson, 1986; 23: Karlsson, 2002. Data for references 9, 16, 17, 18, 21 and 22 came from Nikolov *et al.*, 2004, and have not been consulted directly. Some codes in the figures have been slightly displaced to avoid overlap. All data above 45°N latitude are studies on Northern grey shrike; below, for Southern grey shrike.

[Relación entre la proporción de vertebrados en la dieta de los alcaudones Norteño y Real en Europa, y la latitud a la que el estudio se llevó a cabo. Los resultados se muestran separados para las estaciones de reproducción e invernada. Cuando un estudio tiene datos en ambas estaciones, el código es el mismo en las dos gráficas. Los datos de las referencias 9, 16, 17, 18, 21 y 22 proceden de Nikolov *et al.*, 2004, y no han sido consultados directamente. Algunos códigos en las figuras se han desplazado ligeramente para evitar solapamientos. Todos los trabajos por encima de 45°N de latitud están hechos con alcaudón norteño; por debajo, con alcaudón real.]

they constitute a certain fraction of the shrike diet.

In comparison with previous data on the shrike's diet (both Southern and Northern grey shrike), the most noteworthy aspect is the importance reached by vertebrates, both during the breeding period and during winter (Fig. 1). Vertebrates represented 30–50% of captures for Northern grey shrike during the breeding period in most of the studies analysed (Bohac, 1964; Huhtala *et al.*, 1977; Ruppe and Materna, 1990; Grimm and Haensel, 1991;

Grönlund *et al.*, 1991). In contrast, the data available for Southern grey shrike show a much lower importance of vertebrates, mainly for the northern populations studied by Hernández *et al.* (1993) and Lepley *et al.* (2004). A particular case is the work of Padilla *et al.* (2005) in Canary Islands; these authors suggest that for *L. m. koenigi*, the high importance of lizards *Gallotia galloti* in diet is related with three different ecological factors: the high abundance of these ectotherm vertebrates in island environments, the higher effectiveness of preda-

tion and the lesser investment of energy to capture them. With respect to the data from Budden and Wright (2000) from Israel, they probably overestimate the importance of vertebrates in the diet, since the data refer to nestling chicks, while those of Yosef *et al.* (1991) are lower.

With respect to the winter data, the pattern is similar (Fig. 1): vertebrates are the only food for most of the northern populations of Northern grey shrike (Grönlund *et al.*, 1991; Karlsson, 2002), and their importance diminishes as the latitude lowers (Bassin *et al.*, 1981-1983; Jentzsch and Otto, 1988), whereas for Southern grey shrike, vertebrates represent a very scant part of the diet (Fig. 1), although presumably important for their biomass contribution. Especially in the northern populations, birds and mammals can constitute up to 100 % of captures (Grönlund *et al.*, 1991; Karlsson, 2002), due to the lack of insects during the harsh winters at high latitudes. The exception to this pattern are the works on Northern grey shrike wintering near Frankfurt (Germany) during the winter of 1964 - 1965 by Haensel and Heuer (1970, 1974), which show a diet clearly dominated by invertebrates, mainly Staphilinidae (almost one out of three prey), while vertebrates constitute a minor part of the diet in frequency.

As mentioned above, some authors (Schön, 1998; Hernández, 2000; Lepley *et al.*, 2004) have suggested that the Northern grey shrike preys mainly on warm-blooded prey (birds and mammals) in the cold environments, while the Southern grey shrike relies on cold-blooded ones. However, this proposal refers mainly to vertebrates such as birds and mammals, while lizards are cold-blooded vertebrates. In this sense, the logical expected pattern would be a greater proportion of lizards in the diet at lower latitudes, in the same way as arthropods. The review of the works published to date offer a more complicated scenario. During the breeding period, lizards are conspicuously scarce in the northern populations of Spain (1.4 % frequency in Hernández *et al.*, 1993) and La Crau,

France (0 % in Lepley *et al.* 2004), become important in the diet of the Southern grey shrike in Israel (5.5 % in Yosef *et al.*, 1991, 7.8 % in Budden and Wright, 2000) and Canary Islands (4.5 % in Padilla *et al.* 2005), and reach their highest frequency in Baza and Grao, where they represent 9.7 % and 26.0 %, respectively. Thus, apart of the latitude, the aridity of the sites analysed appear to be decisive: both Israel, Canary Islands and south-eastern Spain are arid zones, while northern Spain and La Crau are much more rainy. Furthermore, in La Crau, lizards are scarce (J. A. Mateo, *pers. com.*), which could explain the low record of captures. Notably, the places in which lizards are important in the diet of the Northern grey shrike during the breeding period are two northern ones, in Finland (26.7 % in Grönlund *et al.*, 1970; 19.7 % in Huhtala *et al.*, 1977), all *Lacerta vivipara*.

A similar pattern appeared when comparing the records from winter. As might be expected, lizards almost disappear in the cold season (but still keep a 13.0 % in Grao during February), and, almost without exception, birds and especially small mammals become the staple food, as latitude increases. The exception is the aforementioned work on the Northern grey shrike of Haensel and Heuer (1970, 1974). These authors mark the winter of 1964 - 1965 as unusually scant in snow, offering an interesting explanation for this outlier: the clear tendency is an increase in vertebrate prey as latitude increases, except when the lack of snow enhances the depredation upon other prey groups such as insects. This reinforces the idea that, more than a clear-cut difference in diet between Northern and Southern grey shrike—the first one capturing mainly warm-blooded prey and the second cold-blooded ones—both species depend on the availability even at a local scale, and such features as snow cover (Haensel and Heuer, 1970), habitat (Hernández, 1995a), or other factors (periods of bird migration; Lorek *et al.*, 2000) may determine a higher or lower use of vertebrates in the diet.

Northern latitudes, with cooler temperatures and snow during winter, have a lower availability of cold-blooded prey; however, when available, they are readily captured. The Southern grey shrike, in turn, inhabits more suitable places for arthropods and lizards than for small mammals, and preferentially preys upon the former, although it is able to change preferences when lizards are scant, as for instance in northern Spain or La Crau.

In conclusion, the proportion of vertebrates found in the diet of the Southern grey shrike appears to be determined much more by prey availability than a special feature of the bird in opposition with the Northern grey shrike. Since Southern localities have lower proportions of birds and small mammals available and higher of insects and reptiles, these latter groups assume more importance in the diet. The fact that both species can switch preferences in response to local circumstances suggests that availability is the key factor explaining the diet of the two shrikes, and hence these dietary differences are the consequence of different prey availabilities in the different areas inhabited, rather than different preferences or hunting strategies.

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