Prey and prey-size selection by the short-toed eagle (*Circaetus gallicus*) during the breeding season in Granada (south-eastern Spain)

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Abstract

The diet of the short-toed eagle (*Circaetus gallicus*) was studied during the breeding season by analysing pellets and remains generated by adults and nestlings. The raptor proved to be a specialist feeder, as snake prey comprised almost 95% of the diet, in both frequency and biomass. We gathered information on prey availability and prey size availability (1499 specimens of nine different species) by searching for snakes in the study area. Regressions of vertebra centrum length and dorsal-scale length on snout–vent length (SVL) of the snakes were used to calculate prey size. The taxonomic diet composition differed depending on the sample analysed – remains or pellets – but we failed to find between-year diet differences. Most of the snakes identified (140 out of 141) belonged to only three species, *Malpolon monspessulanus*, *Elaphe scalaris*, and *Coluber hippocrepis*. Other prey included *Lacerta lepida*, *Natrix maura*, *Bufo bufo*, and *Alectoris rufa*, and many secondary prey (prey from stomach of the prey) were also detected in the pellets. The three main prey species were consumed according to their availability in the study area, but the eagles selected on the basis of prey size. Large snakes within 700–1000 mm SVL were positively selected, whereas snakes under 600 mm SVL were negatively selected. Adult eagles consumed the same prey species as those carried to the nest to feed their single nestling, although prey given to nestlings proved larger in size and biomass, suggesting that adults consumed the smallest prey, reserving the largest for nestlings.

Key words: *Circaetus gallicus*, diet, prey selection, snakes, Spain

INTRODUCTION

The short-toed eagle (*Circaetus gallicus*) presents an unusual case of trophic specialization among raptors, because its diet relies almost exclusively on snakes (Cramp & Simmons, 1980). The Iberian Peninsula has the largest breeding population in Europe, and perhaps in the whole Western Palaearctic (Rocamora, 1994), with an estimated population of between 1700 and 2100 pairs (De Juana, 1989), and a stable breeding population trend (Rocamora, 1994). Many European countries report a marked distribution retreat and population decrease from the nineteenth century onwards (see review in Cramp & Simmons, 1980), due to changes in agriculture, land-use, or to direct persecution (Rocamora, 1994).

Studies on the natural history of the short-toed eagle are not extensive (see review in Del Hoyo, Elliot & Sargatal, 1994), and its feeding habits in Spain have been well analysed only for a population in Sierra Morena (Amores & Franco, 1981). Other information includes anecdotal reports based on scattered data (Valverde, 1967; Irribarren & Rodríguez-Arbeola, 1973; Garzón, 1974; Amores, Franco & Mellado, 1979). This information is either well documented or fragmentary for populations in France (Boudoint *et al.*, 1953; Thiollay, 1968; Choussy, 1973), mainland Italy and Greece (Petretti, 1988; Vlachos & Papageorgiu, 1994), Morocco (Valverde, 1957), and India (Ali & Ripley, 1968), although neither prey nor prey-size selection were considered. At the time of writing, a publication appeared concerning the habitat use and reptilian prey of the short-toed eagle in north-eastern Greece (Bakaloudis, Vlachos & Holloway, 1998), although neither prey type nor prey-size selection is quantified.

In studies of avian foraging, difficulties invariably arise in measuring resource availability (Smith & Rotenberry, 1990). Thus, Rosenberg & Cooper (1990) emphasized the importance of studying resources that can be precisely and easily measured. In this sense, the high trophic specialization of the short-toed eagle (Cramp & Simmons, 1980) makes it suitable for studies of prey selection, since its almost exclusive consumption

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of a single prey type considerably simplifies the task of assessing prey availability (Smith & Rotenberry, 1990).

The existence of a large and stable breeding population of the short-toed eagle in the Depression of Granada (south-eastern Spain), together with the data gathered on the snake population in the same region (Feriche, 1998), enabled us to analyse the feeding ecology of this raptor. We studied its diet during the breeding season in Spain, a period coinciding with the main activity period of the snakes in Mediterranean habitats. The goal of this study was to determine the use of prey resource by this eagle: (1) from a taxonomical standpoint (which of the available prey species are consumed); (2) from a predator/prey size standpoint (which of the available sizes are consumed); (3) to analyse differences in prey type and prey size consumed by adults and nestlings. Finally, we discuss the advantages for this raptor in carrying large snakes to the nest.

METHODS

The study area, located in the province of Granada (south-eastern Spain; 3° 30′ to 4° 18′ W, 36° 50′ to 37° 32′), is 2700 km^2 and ranges from 600 to 1400 m asl in altitude. The climate is typically Mediterranean, with warm, dry summers and mild winters. Average temperatures range from 5.5 °C to 7.8 °C (mean temperature in January), and from 25.7 °C to 26.8 °C (mean temperature in July), and annual rainfall is 460–606 mm irregularly distributed in spring and autumn (standard 30-years meteorological averages; Montero & González-Rebollar, 1982). The 2 years of sampling were climatically similar: mean annual temperature 15.3 °C and 16.0 °C, and annual rainfall 802.4 mm and 687.3 mm in 1996 and 1997, respectively (data from La Cartuja meteorological station, representative of the study area). In terms of flora, the study area is among the most diversified of the regions in the Iberian Peninsula, although the autochthonous vegetation is largely degraded (Rivas-Martínez, 1985). The area is currently characterized by a mosaic of habitats, a landscape positively selected by the short-toed eagle in south-eastern Spain (Sánchez-Zapata, 1999). Short-toed eagle pairs in the study area nested in 3 different biotopes: (1) open pine forest (*Pinus halepensis*, *P. pinaster*); (2) cultivated land with cereal and olive-tree crops; (3) mixed areas of evergreen forest and scrubland (*Quercus rotundifolia*) and cultivated areas, although eagles invariably foraged in opened areas.

The study was carried out during April–August, in 2 successive years (1996 and 1997). At least 11 pairs of short-toed eagles nested in the study area in both years. The diet of these pairs was assessed monthly from pellets and remains collected under the nests and pellets collected under the adults' roosts. Both nests and roosts were cleaned of previous pellets and remains at the beginning of the study. We assumed that mainly nestlings generated pellets and remains under nests (pellets and remains were not sampled under nests during the incubation period), and only adult eagles generated pellets under the roosts, which were far away from the nests. The same has been assumed in similar studies for other raptors (Donázar, 1988). Remains under nests were sometimes complete prey, easy to identify and measure, but most were complete vertebral columns, because nestlings at first are fed by adults tearing-up pieces of snakes. The pellets contained mainly scales.

In remains, snakes were identified to the species level according to vertebrae morphology. For this, we made a reference collection with species from the study area (voucher specimens in the collection of the Department of Animal Biology and Ecology, University of Granada – DBAG), and consulted the literature on this topic (Schneider, 1980; Bailón, 1991; Schatti, 1993; Schleich, Kästle & Kabish, 1996). We also calculated prey size to the nearest 5 mm (snout–vent length – SVL) in the following way. From the species that appeared in the diet, we selected 10 specimens in the reference collection which were representative of the range of sizes of the species. From each specimen, the largest vertebrae were removed, in general those within the first third and the middle of the body.

A reference collection of the scales was made from the same snakes as the vertebrae reference collection (DBAG), by selection of the largest dorsal scales, in general those within the first third and the middle of the mid-dorsal portion of the body. Prey species and prey number (minimum prey number) in pellets were determined according to scale morphology. Because data on scale morphology for Mediterranean snakes are scarce (but see Papageorgiou, Vlachos & Bakaloudis, 1993), we made comparisons with samples from the reference collection. We measured the vertebra centrum length and scale length to the nearest 0.01 mm under a 40 × binocular microscope, using a digital calliper. Relationships between the vertebra centrum length and SVL, and between the scale length and SVL were drawn from the reference collection. The larger collection of snake specimens from the study area (DBAG) was used to establish relationships between SVL and body mass ($n = 603$; Table 1). Non-snake prey were identified using a reference collection from the study area.

Data on taxonomic and prey-size availability were recorded from the Depression of Granada on live and dead snakes (killed by country people, traffic casualties), during standardized searches on 3–4 field days per month (each about 6 h long), throughout the breeding season of the short-toed eagle in the 1987–1997 period (1499 specimens). Voucher specimens are in the Departamento de Biología Animal, University of Granada. In searching for snakes, we did not differentiate among habitats, but as has been demonstrated in Dadia Forest, Greece, the distribution of potential food items in the different habitats is not a good guide to food availability for the short-toed eagle (Bakaloudis *et al.*, 1998). We assumed that the composition of the snake community in the study area remains stable over the years (Feriche, 1998). As the 3 main snake species preyed upon by the

Table 1. Some morphometric relationships of the three main colubrid species that comprise the diet of the short-toed eagle in the Depression of Granada (south-eastern Iberian Peninsula). SVL, VL, and DSL, in mm; BM in g; SEE, standard error of the estimate; SEI, standard error of the intercept; SES, standard error of the slope

	r	*P*	*n*	Relationship	SEE	SEI	SES
Vertebra length (VL) *vs.* body size (SVL)							
Coluber hippocrepis	0.98	0.000	10	SVL = 165.7•VL-54.5	61.2	57.3	11.5
Elaphe scalaris	0.98	0.000	10	SVL = 185.8•VL–35.5	59.0	48.8	10.8
Malpolon monspessulanus	0.98	0.000	10	SVL = 165.7•VL–40.3	54.5	56.5	9.1
Dorsal scale length (DSL) *vs.* body size (SVL)							
Coluber hippocrepis	0.97	0.000	10	SVL = 196.8•DSL–8.2	76.6	61.5	14.2
Elaphe scalaris	0.97	0.000	10	SVL = 159.4•DSL + 3.2	64.1	50.8	10.1
Malpolon monspessulanus	0.98	0.000	10	SVL = 157.3•DSL–96.5	52.4	57.1	8.3
Log body size (logSVL) *vs.* log body mass (logBM)							
Coluber hippocrepis	0.98	0.000	220	LogBM = 2.876•LogSVL–14.26	0.24	0.23	0.03
Elaphe scalaris	0.97	0.000	261	LogBM = 2.832•LogSVL–13.57	0.24	0.26	0.04
Malpolon monspessulanus	0.99	0.000	122	LogBM = 2.872•LogSVL–13.89	0.25	0.27	0.04

short-toed eagle are of similar body size, are mainly diurnal, and have similar seasonal phenology (see review in Salvador, 1997), we also assumed the same probability for them to be found by researchers. A bias is associated with the method – that is, during the mating period (spring and the beginning of summer), the males move more than the females, and thus are more likely to become traffic casualties, or to be found by the researchers (Bonnet, Naulleau & Shine, 1999). As we do not differentiate prey gender, this bias was discarded. In the present study, we were able to determine prey type and prey availability to species level, as well as prey size. This resolved a crucial consideration for many trophic-niche studies – how operationally to categorize food resources. The common trend has been to concentrate on prey-size categories (Sherry, 1990), but here we also were able to consider prey taxa.

Prey frequency was compared by χ^2 contingency tables, and prey selection by the Savage Index, checked for significance with the test of Manly, McDonald & Thomas (1993). Means are followed by ± standard deviation. All variables were tested for normality and homoscedasticity.

RESULTS

Prey identification, prey size calculation, and sample differences

All snake vertebral columns in remains left by the short-toed eagle diet were identified. Relationships between vertebra centrum length and SVL were positive and highly significant for all species in the reference collection (Table 1). Dorsal scales of snake species found showed diagnostic features as follows: *Coluber hippocrepis,* elliptically shaped with two apical pits, and consistently with dark pigmentation derived from the bizarrous dorsal pattern of the species; *Elaphe scalaris,* elliptically shaped with two apical pits and without dark pigmentation; *Malpolon monspessulanus,* pointed with a longitudinal groove in the scales from largest specimens; *Natrix maura*, elliptically shaped and keeled. Relationships between scale length and SVL were positive and highly significant for all species in the reference collection (Table 1). The same was true for the relationship between SVL and body mass when all specimens from the study area in the DBAG collection were considered (Table 1).

The taxonomic diet composition differed depending on the sample, either remains or pellets (*N. maura* and unidentified colubrids were pooled as other colubrids, and all non-colubrids were also pooled; $\chi^2 = 31.8$, 4 d.f., $P < 0.0001$; Table 2). In the results from the remains, there was a bias towards *M. monspessulanus,* although its remains were no more conspicuous than those from other species. Prey size may account partially for this result, as body length varied between snakes in the remains (all species pooled; mean = 878.5 ± 128.4 mm, $n = 70$) and pellets (mean = 775.7 ± 118.1 mm, $n = 136$; t test = 5.58, 204 d.f., $P < 0.001$), *M. monspessulanus* being the longest snake in the study area. As the sample size and prey-type number from pellets were largest with respect to the remains, we therefore used pellets for the analysis of diet frequency (Vlachos & Papageorgiu, 1994; Real, 1996). In addition, we also computed data from the remains, but only for prey size.

Pellets sometimes contained a few fragments of a small saurian (*Psammodromus algirus*, $n = 12$), micromammal fur (*Microtus duodecimcostatus*, $n = 19$), and European wild rabbit remains (*Oryctolagus cunniculus*, $n = 6$). *Psammodromus algirus* and *M. duodecimcostatus* are the main prey for *Malpolon monspessulanus* and *E. scalaris* respectively, and the latter snake frequently preys on rabbits (Díaz-Paniagua, 1976; Pleguezuelos, 1997). Rabbit remains correspond to young specimens < 150 g in biomass, when individuals remain in dens (Soriguer, 1981), and the short-toed eagle cannot prey on them. Therefore, we considered the rabbit remains as secondary prey.

Table 2. Dietary composition of the short-toed eagle in the breeding season (Depression of Granada, south-eastern Iberian Peninsula). Biomass row calculated with data only from pellets. F, frequency of prey; %F, percentage of frequency

	Pellets ($n = 97$)		Remains ($n = 75$)		Biomass
	F	%	F	%	%
Snakes					
Coluber hippocrepis	13	8.7	1	1.3	8.2
Elaphe scalaris	59	39.5	10	13.3	33.7
Malpolon monspessulanus	68	45.6	62	82.6	52.1
Natrix maura	1	0.6	0	0.0	0.2
Unidentified snake	0	0.0	1	1.3	
Total snakes	141	94.6	74	98.6	94.2
Other prey					
Bufo bufo	0	0.0	1	1.3	
Lacerta lepida	7	4.6	0	0.0	4.0
Alectoris rufa	1	0.6	0	0.0	1.6
Total		149		75	

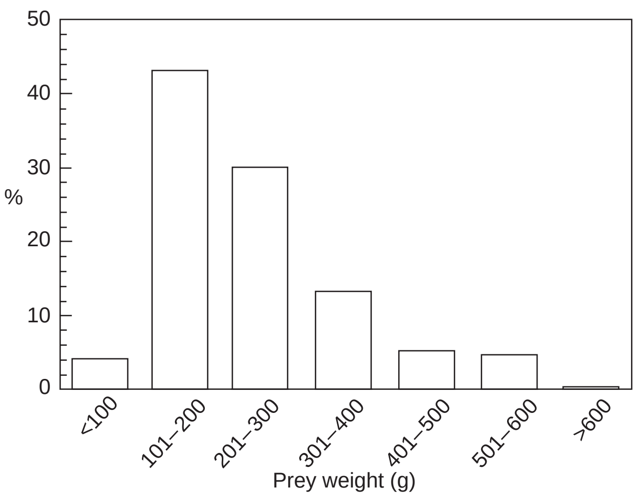

Fig. 1. Prey-mass distribution of short-toed eagle diet in the Depression of Granada (south-eastern Iberian Peninsula); $n = 202$.

Diet

No difference was found in prey frequency between 1996 and 1997 ($\chi^2 = 7.68$, d.f. = 7, $P = 0.17$), so data from both years were pooled. In the study area, the short-toed eagle feeds almost exclusively on snakes, which comprise almost 95% of the diet, both in frequency and in biomass. Almost all snakes consumed (140 out of 141) belonged to only three species, *M. monspessulanus, E. scalaris,* and *C. hippocrepis*. Among the non-snake prey only the ocellated lizard (*Lacerta lepida*), was preyed upon with any frequency and these were invariably adults (Table 2). Average prey mass was 238.6 g ($\pm$ 115.1, $n = 206$; Fig. 1).

Prey selection

The 11 pairs of short-toed eagle examined had consumed only four out of the nine snake species available in the study area. The three main prey species (*C. hippocrepis, E. scalaris, M. monspessulanus*), were consumed according to their availability in the study area (Fig. 2). Analysis of the prey-size availability (when only snakes were considered) gave a rather different picture. The short-toed eagle positively selected snakes within 700–1000 mm SVL, and negatively selected snakes under 600 mm SVL and above 1200 mm SVL. The degree of consumption of the remaining three prey-size class (601–700, 1001–1100, 1101–1200 mm), did not deviate significantly from expected values (Fig. 3). The smallest snake consumed was 465 mm SVL and the largest 1190 mm SVL, both being *E. scalaris*.

Comparison between prey carried to the nest and prey consumed by adults

We found no differences in prey frequency between samples from below the nests and samples below the adults' roosts ($\chi^2 = 6.71$, 5 d.f., $P < 0.24$; Table 3). This result suggests that adults consumed the same prey species as those carried to the nest for feeding nestlings. None the less, prey carried to the nest were larger in size (mean SVL = 836.8 ± 138.9 mm, $n = 125$) and biomass (mean body weight = 264.3 ± 129.8 g, $n = 125$) than those found under the adults' perches (mean SVL = 767.3 ± 105.1 mm, $n = 81$; mean body

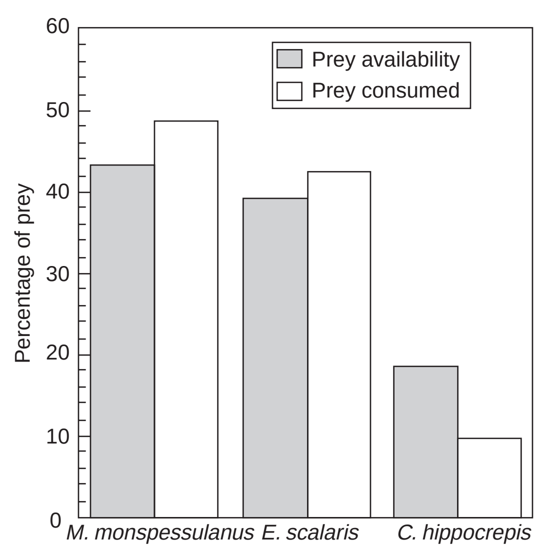

Fig. 2. Snake species selection by the short-toed eagle in the Depression of Granada (south-eastern Iberian Peninsula). Sample size for prey availability: *Malpolon monspessulanus*, $n = 266$; *Elaphe scalaris*, $n = 241$; *Coluber hippocrepis*, $n = 111$. Sample size of the prey consumed in Table 2. All comparisons non significant ($P > 0.05$) according to Manly *et al.* (1993) test: *M. monspessulanus,* 0.85; *E. scalaris,* 0.19; *C. hippocrepis*, 3.28.

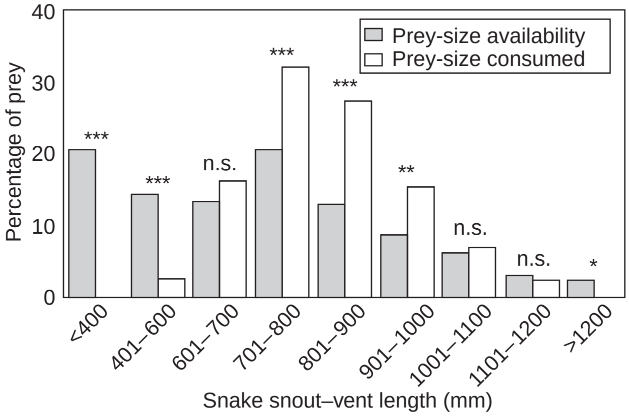

Fig. 3. Prey-size distribution of short-toed eagle diet, and distribution of the available prey size in the Depression of Granada (south-eastern Iberian Peninsula) as compared by the Savage electivity index. Data for the three species as in Fig. 2. Significance level according to Manly *et al.* (1993): *, $P < 0.05$; ** $P < 0.01$; ***, $P < 0.001$; n.s., non-significant.

Table 3. Dietary composition of the short-toed eagle according to the prey found under nests, and prey found under roosts used only by adults (Depression of Granada, south-eastern Iberian Peninsula). F, frequency of prey; %F percentage of frequency

	Nest		Roost	
	F	%F	F	%F
Malpolon monspessulanus	31	58.5	37	42.0
Elaphe scalaris	21	34.4	38	43.1
Coluber hippocrepis	5	8.1	8	9.0
Other prey	4	6.5	5	5.6
Sample size	61		88	

weight = 202.4 ± 77.2 g, $n = 81$; t test significant to $P < 0.001$ level in both comparisons). These results suggest that adults consumed the smallest prey, reserving the largest ones for the nestlings.

DISCUSSION

Our results on the diet of the short-toed eagle in the Depression of Granada coincide with previous information in that the main prey types are snakes or long bodied lizards (Boudoint *et al.*, 1953; Choussy, 1973; Ivanovsky, 1992; Bakaloudis *et al.*, 1998), showing consistency in diet over much of its geographic range. Also in agreement with previous data is that the three main prey species in the Iberian Peninsula are *M. monspessulanus*, *E. scalaris*, *C. hippocrepis* (Garzón, 1968; Pérez-Chiscano, 1973; Irribarren & Rodríguez-Albeola, 1974; Amores & Franco, 1981). Nevertheless, several details differ from data for other areas of the Iberian Peninsula and in other Mediterranean regions. In Western Spain, France, Italy and Greece, the short-toed eagle consumes snakes of smaller body size than those in our study area (*Coronella* spp., *Vipera* spp.; Amores & Franco, 1981; Petretti, 1988; Vlachos & Papageorgiu, 1994). In the same regions, the frequency of lizards in its diet is higher, with the consumption of lizards of small body size (*Podarcis muralis, Podarcis taurica, Psammodromus algirus, Chalcides chalcides*; Petretti, 1988; Vlachos & Papageorgiu, 1994). Finally, in other regions of the distribution area of this eagle, the consumption of small snakes and lizards and several invertebrates, has been also reported (Valverde, 1957; Ali & Ripley, 1968; Garzón, 1974). Such differences in snake-prey sizes are surprising, because all northern Mediterranean peninsulas are inhabited by vicariant species or subspecies of snakes quite similar in body size (Gruber, 1989). Considering the other small-bodied prey cited in the literature (small lizards, invertebrates; in all cases coming from pellet analysis), and taking into account the large amount of secondary prey found in our sample, we deduce that some of the small prey cited in the diet of the short-toed eagle are simply secondary prey. Cramp & Simmons (1980) also stated that the invertebrates recorded as prey by some authors sometimes derive from the stomachs of prey.

In the study area the short-toed eagle consumed almost exclusively three out of the nine snake species that inhabit southern Spain, and those species were preyed upon according to their availability. The analysis of the prey-size selection provided insights into prey-species selection and the lack of some snake species. The eagle selected medium to large sized snakes, and rejected snakes < 465 mm SVL, this being a body size rarely or never reached by four of the rejected species (*Coronella austriaca, C. girondica, Macroprotodon cucullatus, Vipera latasti*). The maximum body size of *N. maura* is slightly above the minimum prey size accepted by the eagle (see review in Salvador, 1997), but *N. maura* spends much time in water, and so may evade hunting eagles (Bakaloudis *et al.*, 1998). Finally, the ninth species, *Natrix natrix*, has a body size largely overlapping the prey-size spectrum of the short-toed eagle, and is the main prey species for the raptor in other European countries (Boudoint *et al.*, 1953; Petretti, 1988; Vlachos & Papageorgiou, 1994; Bakaloudis *et al.*, 1998). However, in southern Spain *N. natrix* occupies mountain habitats (Pleguezuelos, 1989) that scarcely coincide with the altitude distribution of the short-toed eagle (García & González, 1997).

The only non-snake prey significantly consumed by the short-toed eagle is the ocellated lizard, as found in Doñana marshland and Sierra Morena (southern Spain; Valverde, 1967; Amores & Franco, 1981). This is the largest lizard in Europe, with an average body mass of 175 g (J. A. Mateo, pers. comm.), and it is therefore close to the average body mass of the snakes consumed by the eagle.

The analysis of prey-size indicated that the eagle actively selected medium to large prey with respect to prey-size availability (Fig. 3). Daily biomass requirements for nestlings were estimated at 120–125 g (Boudoint *et al.*, 1953; Thiollay, 1968), or up to 215 g/day for nestlings in the last developmental stage (Petretti, 1988). If we assume that the last figure is close to adult daily requirements, the biomass consumed by a breeding unit (two adults plus one nestling) would represent up to 645 g/day. This high amount may explain the preferred predation upon large snakes, as the short-toed eagle tends to optimize prey size (Stephen & Krebs, 1986). Smaller prey would require much time and energy in searching with respect to the energy intake.

The short-toed eagle is an active forager that spends much time quartering the ground searching for prey (Brown & Amadon, 1968), and has perhaps the largest home range within the community of diurnal raptors in the Iberian Peninsula (Veiga, 1982; Sánchez-Zapata, 1999). Snakes larger than those consumed would increase handling time and would even be potentially dangerous (see also Bakaloudis *et al.*, 1998). The largest individuals of the three main species preyed on are highly aggressive and one (*M. monspessulanus*) is a rear-fanged venomous snake (Pleguezuelos, 1997). Thus, the largest sizes might have been avoided even though they represented the largest biomass intake.

We conclude that despite the pronounced estenophagy for snakes, the short-toed eagle behaves as a taxonomical generalist within this prey type, and only selects optimal prey sizes whatever the species.

When we differentially analysed the diet between adults and their single nestling, we again failed to find a shift in prey type, as the differences referred only to prey size. Moreover, in the first nestling growth period, adults also feed on the prey carried to the nest (Petretti, 1988; L. F. López-Jurado, pers. comm.); therefore, the difference between prey size carried to the nest and prey size that adults select for their own consumption must be more pronounced than reflected by our data. This may be related to the finding that in central Italy the short-toed eagle carried only snakes to the nest, normally well-sized individuals, although adult eagles also consumed other non-snake and small-sized prey types (Petretti, 1988). Differences between prey carried to nest and prey consumed by adults has been reported in other raptor species (Rudolf, 1982; Massman *et al.*, 1986; Donázar, 1988). These differences may arise from the balance between costs and benefits inherent to the hunting activity: only prey of suitable size are carried to the nest, thereby saving time, energy, and risks related to overly frequent visits to the nest to deliver prey that are too small (Curio, 1976; Veiga, 1982).

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