

**FEEDING HABITS OF THE COMMON CHAMELEON,
CHAMAELEO CHAMAELEON (LINNAEUS, 1758) IN THE
SOUTHEASTERN IBERIAN PENINSULA**

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ABSTRACT

We present the feeding habits of the common chameleon (*Chamaeleo chamaeleon*) at Taramay, a small coastal valley in the southeastern Iberian Peninsula. Fecal pellets collected from sexed and measured specimens trapped in the field were used for diet analysis. Thirty-four fecal samples provided a total of 777 identified prey items. All prey were arthropods and the numerically dominant groups were Diptera, Hymenoptera, Orthoptera, and Heteroptera. We failed to find sexual differences in diet preference, but there was a seasonal shift in the prey consumed. Orthoptera, the largest prey type, was consumed less in spring than summer or autumn. Examination of grasshopper phenology in coastal habitats of the southeastern Iberian Peninsula, and of the change in chameleon habitat utilization and mobility during the mating period, verified that the common chameleon appears to consume grasshoppers in approximate proportion to their abundance. Prey consumed were smaller than in previous studies. We believe the earlier findings may have been biased due to the diet consisting of captive specimens. Most of the prey consumed in the present study were flying insects, perhaps reflecting the arboreal habits of this climbing species; and most prey were also mobile, as has been predicted for sit-and-wait foragers such as the common chameleon.

INTRODUCTION

The common chameleon, *Chamaeleo chamaeleon* (Linnaeus, 1758), is distributed in the southern tip of the Iberian Peninsula, the northern border of Africa, several islands of the Mediterranean, Turkey, and to the western part of the Middle East (Martin, 1992). In the Iberian Peninsula its distribution is over a very narrow band, both in latitude and altitude, close to the sea shore from southwest to southeast (Blasco, 1997a). Within this band, the populations are restricted to only a few places, isolated from each other. Apart from the population in the eastern part of Málaga province, other populations correspond to recent (20th century) anthropogenic introductions, and there is a controversy regarding the indigenous status of the Iberian populations (Blasco, 1997b). The only fossil remains

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found so far in the Iberian Peninsula date to the Bronze Age (Cueva del Higuero, Málaga province; Talavera and Sanchíz, 1983), a period when humans are known to have crossed the Straits of Gibraltar. Thus, the presence of *C. chameleon* in the north-western Mediterranean may well have resulted from human transport. The same is probably true for several Mediterranean islands that the species currently inhabits (Luiselli and Rugiero, 1996; Schleich et al. 1996). The lack of morphological (Blasco et al., 1985a) and biochemical (starch gel electrophoresis: Hofman et al., 1991; mitochondrial DNA sequencing: J.A. Mateo, pers. comm.) differences between Iberian and Moroccan populations, supports this hypothesis.

This species is the only strictly arboreal European reptile, and many studies have focused on its morphology, reproductive ecology, and behavior (see revisions in Klaver, 1981; Salvador, 1997a). Despite the peculiar habitat selection of *C. chameleon* compared with other European reptiles, and the specialized hunting technique that chameleons show in general, little information is available regarding its feeding habits in the wild. To our knowledge, the diet of this species has only been studied in northern Africa (two small samples from Libya; Burmeister, 1989) and in Malta (Luiselli and Rugiero, 1996), mainly by analysis of fecal pellets; there are also some anecdotal reports (Werner, 1929; Mosauer, 1934; Bons, 1967). However, references are more numerous concerning the feeding habits of the species in captivity (Fisher, 1882; Schreiber, 1912; Lantz, 1924; Rehacek, 1928; Klein, 1931; Werner, 1949; Blasco et al., 1985b; González de la Vega, 1988; Rogner, 1992; Henkel and Heinecke, 1993).

Here we report on the feeding habits of a small and isolated population of *C. chameleon* from the southeastern Iberian Peninsula. The diet was studied in relation to season and to sex of the specimen. We discuss the seasonal shift in the prey consumed in relation to the chameleon's reproductive cycle and the phenology of its main prey-type in adjacent coastal habitats. We also compare our data on prey size with the findings of other studies.

MATERIALS AND METHODS

Field work was carried out during 1996 in the locality of Taramay (Almuñecar, Granada province; 36°45'N, 3°39'E), a small valley crossed by a seasonal watercourse and situated at 120 m above sea level. The climate is Mediterranean, with warm, dry summers and mild winters. Mean minimum temperature in winter (January) is 8.0 °C, mean maximum temperature in summer (July) is 29.1 °C, and mean annual temperature is 18.5 °C. Annual rainfall averages 480 mm, irregularly distributed in spring and autumn (1945–1975 period; Castillo, 1989). The study plot was a steep slope, 8 ha in area, occupied by abandoned stands of fruit trees (*Annona chirimoya*, *Ceratonia siliqua*, *Olea europaea*, *Persea americana*, *Prunus dulcis*, *Punica granatum*) 3–6 m high, together with scattered shrubs of natural vegetation (*Maytenus senegalensis*, *Spartium junceum*, *Thymelaea hirsuta*) 0.7–2.0 m high.

Fecal samples were our only source of diet data. The chameleons were collected from the study site by two observers for two days per month (5 hr/day) from March to October, the main activity period of the species at this site (pers. observ. of the authors). To minimize violating the independence of the samples, we always trapped chameleons in the same places and for the same amount of time. Thus, we assumed that there was a similar chance of re-trapping any one individual. Specimens were measured (snout to vent length: SVL and tail length: TL) with a caliper to the nearest millimeter. Each individual was kept separately in a terrarium until it defecated, and then returned to the collection site. Specimens were sexed according to color (Cuadrado, 1998; our data), SVL/TL relationship (Blasco et al., 1985a), and the presence of hemipenial pockets. In addition, we collected fecal pellets from previously selected and cleaned spots. The feces of other lizard species present at the sampling plot clearly differed from those of adult chameleons, either in size (*Chalcides bedriagai*, *Psammodromus algirus*), in size and color (*Tarentola mauritanica*), or in shape (*Lacerta lepida*).

In the laboratory, the feces were dissected and prey were sorted, identified to the lowest taxonomic level possible, and measured (± 0.1 mm) under a binocular microscope 10–40 $\times$ equipped with a micrometer. Measurement of characteristic body parts (mandible width in Orthoptera; head width in Coleoptera, Diptera, Heteroptera, Hymenoptera, Mantodea, and Odonata; prosome width and chelicera length in Araneae; Hódar, 1997) enabled us to estimate the length and biomass of the prey, using a series of regression equations prepared from arthropods caught in southeastern Iberian Peninsula (Hódar, 1996, 1997). When prey was identifiable but not measureable (3.9% of the prey items, mostly Diptera), we assigned it the average length and biomass recorded in the feces for that prey type during the same season of the year.

Diet analysis was performed on a seasonal and sexual basis, and summarized in two different ways: frequency (number of prey belonging to a given prey type) and estimated biomass (dry biomass in mg). We tested for sexual differences in diet by analyzing fecal samples from individuals of known sex (five males, six females) during the same season (spring), thereby avoiding bias produced by seasonal shift in the diet (see results). In order to determine the extent of specialization on different prey by any one individual, we generated average and standard deviation values per individual (per feces) for every prey type. We compared taxonomic composition between seasons with the Kruskal–Wallis test; because of the small sample size during some seasons, we also used Dunn's test for paired comparison. In addition, we took each individual chameleon fecal pellet as a replicate for analysis of prey size. We thus calculated average prey size per individual, and then the average prey size across the individuals for each group analyzed (either season or sex). Comparison of prey length (log-transformed) between seasons was performed with a nested ANOVA. When the same test was applied several times on the same data basis, we applied a sequential Bonferroni correction to the significance of the test (Rice, 1989).

RESULTS

The studied population of *C. chamaeleon* was small. During 1996, after 167 hours of field sampling, we succeeded in trapping only 21 chameleons, from which we obtained the same number of fecal pellets, in addition to 13 pellets collected on the ground that could be unequivocally assigned to this species. All of the individuals were large enough (SVL, mean $\pm$ SD = 121.1 $\pm$ 15.9 mm, range = 92–150 mm, n = 21) to be considered adults (Blasco et al., 1985a). Although we lack quantitative data, fecal pellets collected on the ground did not differ in size (as estimated visually) from those obtained from specimens kept temporarily in terraria, and we assumed that they also originated from adult specimens.

The fecal sample analysis provided a total of 777 identified prey items. The number of prey in each fecal pellet ranged from 5 to 74 (mean $\pm$ SD = 23.5 $\pm$ 15.8, n = 33). Based on feces analysis at the study site, *C. chamaeleon* fed exclusively on arthropods. Diptera (flies) were the most frequently consumed prey types, with Hymenoptera (mostly bees and wasps, some ants), Heteroptera (bugs), and Orthoptera (grasshoppers) being next in

Table 1

Prey items identified from the fecal pellets of *Chamaeleo chamaeleon* in Almuñecar (Granada, southeastern Spain) during 1996 according to season of the year. Data are presented as mean and standard deviation of the percentage of numeric frequency (%F) in each season, and numeric frequency and biomass (%B) for the three seasons pooled (total). *Significance after Bonferroni sequential correction

Prey taxon	Spring	Summer	Autumn	Krus.-Wall.		Total	
	%F	%F	%F	d.f.	<i>p</i>	%F	%B
Phylum Chelicerata							
Aracae ¹	1.0 $\pm$ 1.9	1.5 $\pm$ 1.3	2.3 $\pm$ 2.9	2	0.008*	7.2 $\pm$ 10.9	1.3 $\pm$ 2.0
Phylum Uniramia							
Odonata ²	0.3 $\pm$ 1.4					0.1 $\pm$ 0.4	0.2 $\pm$ 1.1
Orthoptera ³	8.7 $\pm$ 19.5	49.5 $\pm$ 36.7	43.2 $\pm$ 35.5	2	0.003*	10.6 $\pm$ 17.8	22.5 $\pm$ 31.4
Mantodea ⁴	1.7 $\pm$ 5.8					0.3 $\pm$ 1.2	1.1 $\pm$ 4.6
Heteroptera ⁵	14.3 $\pm$ 19.7	26.7 $\pm$ 25.8	22.6 $\pm$ 30.3	2	0.066	11.9 $\pm$ 13.5	18.2 $\pm$ 22.6
Coleoptera ⁶	7.0 $\pm$ 6.5	2.7 $\pm$ 1.6	3.1 $\pm$ 2.7	2	0.77	8.0 $\pm$ 7.5	5.5 $\pm$ 5.6
Lepidoptera ⁷	4.8 $\pm$ 21.8					3.0 $\pm$ 17.4	3.0 $\pm$ 17.4
Diptera ⁸	29.6 $\pm$ 30.7	4.3 $\pm$ 6.3	17.7 $\pm$ 34.4	2	0.42	30.7 $\pm$ 31.7	22.4 $\pm$ 29.2
Hymenoptera ⁹	32.6 $\pm$ 21.6	15.3 $\pm$ 13.1	11.4 $\pm$ 8.0	2	0.39	28.2 $\pm$ 19.8	25.7 $\pm$ 20.5
Prey identified	414	203	160			777	
Biomass							
(mg dry weight)	5891.8	5995.8	2787.8			14675.2	
Prey length							
(mean $\pm$ SD)	9.3 $\pm$ 2.2	12.3 $\pm$ 3.6	10.1 $\pm$ 2.0				
Number of feces	21	7	6			34	

Identified families ranked according to importance within each order: ¹Araneidae; ²Lestidae; ³Acrididae; ⁴Mantidae; ⁵Pentatomidae, Lygaeidae, Reduviidae; ⁶Buprestidae, Curculionidae, Ccrambicidae; ⁷Pieridae; ⁸Muscidae; ⁹Apidae, Vespidae, Formicidae, Sphecidae, Chrysididae.

frequency. In contrast, three other prey species (caterpillars, praying mantis, dragonflies) were found only in insignificant numbers. An analysis of the biomass contributed by each prey type to the diet, however, revealed the most important prey species to be Hymenoptera, followed by Orthoptera (both large organisms) and Diptera (Table 1).

The common chameleon consumed prey ranging from 1.1 to 44.0 mm in length, and from 0.1 to 475.2 mg in mass (dry weight), with the smallest being flies and the largest grasshoppers. Mean prey size was 10.1 mm (SD = 2.7, $n = 34$), and mean prey dry mass was 20.9 mg (SD = 17.2, $n = 34$). Organisms ranging from 3 to 12 mm in length comprised more than 75% of the prey consumed (Fig. 1).

No sexual differences were observed in choice of prey (Mann–Whitney U test, $0.9 < p > 0.1$; Odonata and Mantodea grouped in this analysis) or in prey size (nested ANOVA, $F = 0.44$, 1 d.f., $p < 0.50$) (Table 2); but there was a high variability among individuals in the size of the prey consumed (nested ANOVA, $F = 2.93$, 9 d.f., $p < 0.003$).

We tested for seasonal differences in diet, grouping sexes by analyzing fecal samples from three seasons (spring, summer, autumn). The diet was not homogeneous throughout the year for spiders and grasshoppers (Table 1; Lepidoptera, Mantodea, and Odonata grouped in this analysis), and a posteriori paired comparisons found differences between spring and summer (Dunn test, $Q = 2.58$, $p < 0.05$), with more of both prey types being consumed in summer. The significance of grasshoppers in the spring diet was almost negligible, whereas in summer they were the most frequently consumed prey, representing nearly 50% of the total prey mass. In autumn their importance decreased slightly compared with summer (Table 1). In parallel with the seasonal shift in the type of prey

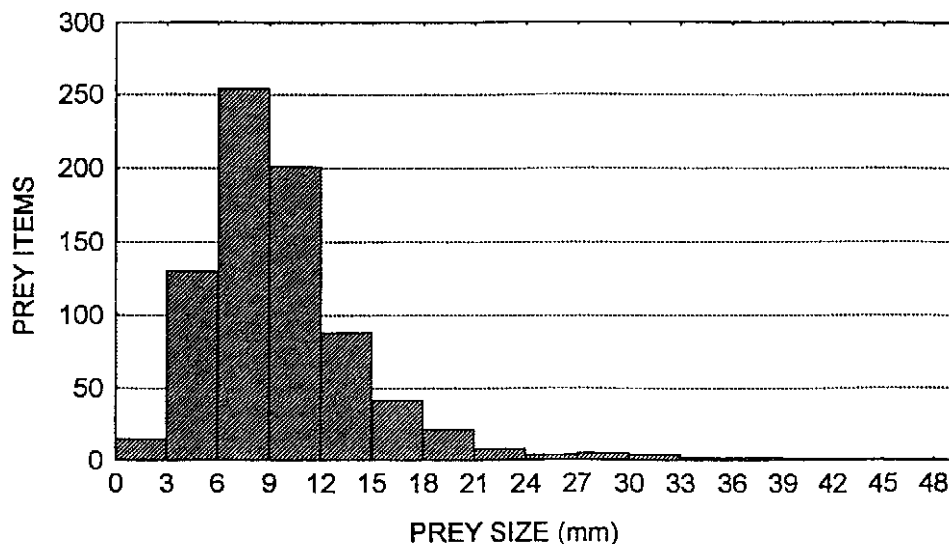


Fig. 1. Size distribution of prey obtained from 34 fecal pellets of *Chamaeleo chamaeleon* in Almuñecar (Granada, southeastern Spain). $n = 777$ prey items.

Table 2

Prey items identified from fecal pellets of *Chamaeleo chamaeleon* in Almuñecar (Granada, southeastern Spain; spring 1996) according to sex. Data are presented as mean $\pm$ standard deviation of the percentage of numeric frequency. p = significance of the difference between sexes (Mann-Whitney U test)

Prey Taxon.	Males %F	Females %F	p
Phylum Chelicerata			
Araneae	8.6 $\pm$ 9.2	8.8 $\pm$ 13.9	0.78
Phylum Uniramia			
Odonata	0.5 $\pm$ 1.2		
Orthoptera	0.7 $\pm$ 1.6	5.6 $\pm$ 6.2	0.31
Mantodea		1.0 $\pm$ 2.4	
Heteroptera	17.0 $\pm$ 9.8	13.4 $\pm$ 12.7	0.20
Coleoptera	13.2 $\pm$ 10.5	12.7 $\pm$ 8.2	0.41
Diptera	12.5 $\pm$ 18.0	16.8 $\pm$ 13.2	0.58
Hymenoptera	47.5 $\pm$ 14.3	41.7 $\pm$ 21.7	0.12
Prey items	126	73	
Number of feces	5	6	

consumed, a seasonal shift in prey length was also detected (nested ANOVA, $F = 4.93$, 2 d.f., $p < 0.0001$), in spite of the variability in the length of the prey consumed by the different individuals (nested ANOVA, $F = 4.17$, 31 d.f., $p = 0.0001$).

DISCUSSION

Our results are generally consistent with previous reports on the feeding habits of *C. chamaeleon* in the wild. The main prey in the diet of common chameleons from northern Libya (Hymenoptera, Coleoptera, Diptera; Burmeister, 1989) and Malta (Orthoptera, Cicadidae, Cimicomorpha; Luiselli and Rugiero, 1996) were also the main prey of chameleons in the southern Iberian Peninsula (present study). The two earlier studies reported remains in fecal pellets which were not found in any samples in the present study. In northern Libya, some vegetal remains (seeds, leaves, flowers, leaf buds) were consistently present in samples, and in Malta a small endemic saurian (*Podarcis filfolensis*) appeared in half of the stomachs dissected and six out of the 34 fecal pellets analyzed. Burmeister (1989) attributes the appearance of vegetal remains to failed feeding attempts and to secondary feeding by the insect prey (see also Bustard, 1963), and doubts that chameleons directly seek flowers or seeds as food. Although we found no vertebrate prey in the samples studied, predation upon most of the small saurians that inhabit the region (*Psammodromus algirus*, *P. hispanicus*, *Acanthodactylus erythrurus*, young *Lacerta lepida*), as well as upon hatchling birds, has been reported for captive

specimens from the southwestern Iberian Peninsula (González de la Vega, 1988). Predation upon small saurians has also been reported in studies of the natural history of the species in Tunisia, Israel, and Morocco (Mosauer, 1934; Werner, 1949; Bons, 1967).

Studying diet by fecal analysis may have an inherent bias, as it can fail to identify soft-bodied prey. Caterpillars and slugs are frequently eaten by some chameleons in Africa (Martin, 1992; Necas, 1995), but neither prey type was found in our study. Caterpillars, however, have sclerotized parts, such as the head and mandibles, and our fine-tuned analysis would have revealed their existence. Indeed, we easily identified chelicera of another soft-bodied prey type, the spider. Furthermore, there are no aerial slugs in the study area, which is too dry for these gasteropods (our data). In addition, we believe that lizards as a possible prey were not overlooked by our method because some of their bones (i.e., mandibles) have been found in the fecal pellets of other reptile species, and are easily recognized (J.A. Hódar, pers. comm.). In general, fecal analysis not only provides accurate information on diet (Fitch, 1987; Tucker and Fitzsimmons, 1992), but is also particularly useful when working with endangered species, such as the common chameleon.

The major differences between our findings and those of others on the diet of *C. chameleon* concern prey size. The average prey length of chameleons in the southern Iberian Peninsula was under 10 mm, and 90% of the prey items were under 15 mm in length (Fig. 1). Although data on prey length are scarce in the literature, Blasco et al. (1985b) reported 3–4 cm as the average prey length in specimens held in semi-natural conditions. The three main prey types found by Luiselli and Rugiero (1996) in the Maltese population were usually all larger than 10 mm (Cicadidae, Orthoptera, and small saurians); and the sole prey for which Burmeister (1989) gave a size was > 40 mm in length (Soliphugae). Other sources report mainly large prey in the food spectrum of *C. chameleon* (Schreiber, 1912; Lantz, 1924; Werner, 1929; Mosauer, 1934; Bons, 1967), and none cite prey as small as 1 mm, such as those found in the current study. On the basis of data gathered from specimens in captivity, we suspect that prey size was previously overestimated by offering chameleons only large and colorful prey. On the other hand, small prey may have gone unnoticed in these previous studies. The small size of most prey items, combined with the high numbers of prey items per fecal pellet, suggests that common chameleons may rely on frequent small meals, rather than feeding infrequently on large prey. In this respect, *C. chameleon* resembles most other small lizards (Pianka, 1986). The matter of tiny prey, which demands a greater number of feedings, is also interesting in view of the high energetic cost of tongue projection in chameleons (Wainwright and Bennett, 1992).

The lack of any gender-related preferences in diet could be a consequence of the minimal sexual dimorphism in body size that this species shows (Blasco et al., 1985a; Schleich et al., 1996; C. Díaz-Paniagua and M. Cuadrado, unpubl. data). Nevertheless, because of the small sample size in this analysis, we must consider this result only as tentative.

Flying insects such as Muscidae, Apidae, Vespidae, Lygaenidae, Cerambycidae, and Buprestidae are better represented in the diet of the common chameleon, a climbing

lizard species, than they are in terrestrial lizard species of the Iberian Peninsula (Salvador, 1997b). The seasonal analysis of diet also confirms that this species is arboreal throughout most of the year. The most important ground-dwelling prey type was Orthoptera (most of the grasshoppers consumed belonged to geophilous genera: *Sphingonotus*, *Oedipoda*, *Acrotylus*, *Pezotettix*, *Dociostaurus*). According to our results, the main seasonal shift in diet related to Orthoptera. Grasshoppers were rarely consumed in spring, when chameleons are strictly arboreal (observations of the authors at the study site), but they were the main food source in summer and autumn, which agrees with the phenological peaks of Orthoptera as reported in studies carried out close to our own study site (Aguirre and Pascual, 1988; Badih et al., 1997). Moreover, mating of the common chameleon occurs in summer, when the males descend from the trees or bushes and move around on the ground in search of a mate among the females, which do not become total ground dwellers, but tend to occupy a lower layer of the vegetation, such as among grass stalks (Blasco et al., 1985b). In late summer and early autumn, the females also descend from the trees or bushes for oviposition in the ground (Bons and Bons, 1960; Blasco et al., 1985b). Our results on the seasonal feeding habits of the common chameleon suggest that it feeds after leaving the trees during the reproductive season.

Many of its prey types are quite mobile (Muscidae, Formicidae, Sphecidae, Vespidae, Apidae, Pentatomidae, Cerambicidae; see also Blasco et al., 1985b). Foraging theory suggests that sit-and-wait species tend to encounter and eat fairly mobile prey, compared with more active widely foraging species (Pianka, 1986). Our observations on foraging, and those from M. Cuadrado (pers. comm.) in southwestern Spain, confirm that *C. chameleon* is a sit-and-wait species, as most chameleons are (Bustard, 1963; Burrage, 1973; Blasco et al., 1985b; but see Necas, 1995). Sit-and-wait species also tend to be less visible to predators and this, combined with the chameleon's slow locomotion and camouflage ability, would appear to contribute to this peculiar lizard's ability to avoid predators.

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