Journal of Biological Research-Thessaloniki **16**: 166 – 176, 2011
J. Biol. Res.-Thessalon. is available online at http://www.jbr.gr
Indexed in: WoS (Web of Science, ISI Thomson), SCOPUS, CAS (Chemical Abstracts Service) and DOAJ (Directory of Open Access Journals)

Feeding habits and provisioning rate of breeding short-toed eagles *Circaetus gallicus* in northeastern Greece

Dimitrios E. BAKALOUDIS[1*] and Christos G. VLACHOS[2]

[1] *School of Animal & Microbial Sciences, University of Reading, Whiteknights PO Box 228, RG6 6AJ Reading, UK*

[2] *School of Forestry & Natural Environment, Aristotle University of Thessaloniki, PO Box 241, 540 06 Thessaloniki, Greece*

Received: 12 February 2010 Accepted after revision: 30 July 2010

The diet of the short-toed eagle (*Circaetus gallicus*) was studied in the Dadia-Lefkimi-Soufli National Park in northeastern Greece during the breeding seasons of 1996-98. From 167 pellets analysed, 236 prey items were identified. Snakes (84.3%) were the main prey of adult eagle diet, followed by rodents (5.6%), lizards (4.2%), tortoises (3.8%) and other miscellaneous prey items. Grass snakes and large whip snakes comprised over 80% of the snakes. Four nests were monitored during the brooding period to record the prey size and type, the feeding behaviour and the prey delivery rate. The male provided most of the food, whereas the female cared for the young by brooding, shading and feeding. Colubrids comprised the principal prey brought to the nests, both in terms of frequency of occurrence (79.3%) and biomass (88.9%). Most snakes and European glass lizards brought to the nests measured between 60 and 120 cm in length. Both nestling and adult birds showed a narrow dietary breadth. Although there were no differences among the seven 10-day stages of young growth, neither in the prey delivery rate (mean: 1.13 prey item day^{-1}), nor in the prey biomass delivered per day (mean: 211.3 g day^{-1}), there was, however, a significant variation in the daily food biomass consumed by the nestling over the brooding period (mean: 174.8 g day^{-1}). The daily prey delivery rate was unimodal in frequency, peaking between 09:00 and 12:00, and was synchronised with the diurnal activity pattern of reptiles which constituted the bulk of the short-toed eagle diet.

Key words: short-toed eagle, *Circaetus gallicus*, diet, feeding behaviour, prey delivery.

INTRODUCTION

The short-toed eagle (*Circaetus gallicus,* GMELIN 1788) is the only representative of snake eagles that breeds in the Palearctic (Cramp & Simmons, 1980). It displays little reversed sexual dimorphism, with males only slightly smaller than females, and this may be linked to the particular diet of the species (Newton, 1979). Most of the breeding range of short-toed eagle encompasses temperate environments, particularly when these can provide both suitable forested habitats for nesting (Bakaloudis *et al*., 2000; 2001), and open habitat types including grasslands and cultivated areas for foraging (Bakaloudis, 2009). Preferences for open foraging habitats likely to reflect both abundance of prey species (reptiles) (Newton, 1979) and suitable vegetation structure to approach easily the reptilian prey (Preston, 1990).

Environmental quality can affect the size of raptor populations through food supply, nest sites and human activities (Newton, 1979). In order to take measures to conserve a raptor population, information on its preferred prey, nesting site and the extent to which human activity affects prey availability is required. Food habits of short-toed eagles have previously been studied in Spain (Amores & Franco, 1981;

* Corresponding author: tel.: +30 25210 60471, e-mail: dimbak@teikav.edu.gr
Present address: Technological Educational Institute of Kavala, Department of Forestry & Management of Natural Environment, Laboratory of Wildlife Ecology & Management, 1st km Drama-Mikrohori, 661 00 Drama, Greece

Gil & Pleguezuelos, 2001; Moreno-Rueda & Pizarro, 2007), France (Boudoint *et al.*, 1953; Thiollay, 1968; Choussy, 1973), Italy (Petretti, 1988), Greece (Vlachos & Papageorgiou, 1994), Belarus (Ivanovsky, 1992), Hungary (Becsy, 1971) and Germany (Reichholf, 1988). A variety of methods have been used to study diet; a few studies have been based largely on analysis of stomach contents (Thiollay, 1968), but most studies have depended on interpretation of pellet contents and prey remains. Some studies have also been carried out using direct observations from blinds to assess the diet of the young (Boudoint *et al.*, 1953; Becsy, 1971; Choussy, 1973; Ivanovsky, 1992), but none include a comparative analysis between prey consumed by nestlings and adults.

In this study we report the feeding habits of breeding short-toed eagles, the numerical and biomass contribution of prey items to the diet, prey delivery rate and prey consumed by nestlings and adults.

MATERIALS AND METHODS

Study area

The study was conducted within the Dadia-Lefkimi-Soufli National Park (DLS NP hereafter), located in northeastern Greece (40°59′-41°15′ N, 26°19′-26°36′ E), from 1996 to 1998. The DLS NP is crisscrossed by steep valleys and gullies, with elevations ranging from 20 to 700 m above sea level. The climate is sub-Mediterranean, with dry, hot summers and wet, cold winters with an average annual precipitation of 664 mm. The area is characterised by a variety of habitats, ranging from low-lying scrublands where *Phyllirea media* and *Arbutus andrachne* shrubs predominate, grasslands with scattered *Juniperus oxycedrus* or trees, to forested hillsides containing a mixture of coniferous (*Pinus brutia* and *P. nigra*) and deciduous (*Quercus* spp.) plant associations. Most of the area is forested (61%) or partially forested (16%), while the remaining is cultivated land (21%) and barren (2%) (Bakaloudis, 2000).

The study area, which was established as a Wildlife Reserve in 1980, has been declared a National Park (433 km^2) in 2006, accommodating one of the largest raptor assemblages in Europe. The area holds on average one short-toed eagle pair per 16.9 km^2 (Bakaloudis *et al.*, 2005). The diverse herpetofauna includes common reptiles like grass snake (*Natrix natrix*), dice snake (*Natrix tessellata*), Montpellier snake (*Malpolon monspessulanus*), large whip snake (*Coluber caspius*), Dahl's whip snake (*Coluber najadum*), Aesculapian snake (*Elaphe longissima*), nose-horned viper (*Vipera ammodytes*), European glass lizard (*Pseudopus apodus*), green lizard (*Lacerta viridis*), Hermann's tortoise (*Testudo hermanni*), and spur-thighed tortoise (*Testudo graeca*) (Helmer & Scholte, 1985; Bakaloudis *et al.*, 1998; Kati *et al.*, 2007).

Data collection

The feeding habits of short-toed eagles were determined during the breeding seasons of 1996-98, using three methods: a) collection of prey remains, b) pellet collection, and c) direct observations at four nests each with one eaglet (Rosenberg & Cooper, 1990; Marti *et al.*, 2007). Methods (a) and (b) were used to assess the diet of adults, whereas method (c) was used to identify prey species eaten by the eaglet and to estimate prey delivery rate, prey biomass delivered to the nests and prey biomass consumed by the chick.

Prey remains and pellets were collected from nests and roosts ($n = 22$ nesting territories). Successful territories were regularly visited once every 15 days, and intensive searches were carried out below nesting trees or at roosts within a radius of approximately 100 m from the nest. Most pellets (92%) were collected below roosting trees, the rest below nesting trees.

Pellets were stored individually in plastic bags and classified by nest and collection date to enable comparison of diets between nests and between breeding stages. Reptiles represented in the pellets were identified by microscopic examination of the scales, by comparison with a reference collection, and with an identification key (Papageorgiou *et al.*, 1993). Mammals were identified to genus by microscopic examination of hair morphology and the use of a key (Papageorgiou *et al.*, 1991).

The diet of young short-toed eagles was assessed by direct visual observation at four nests from nearby hides (one in 1996, two in 1997, one in 1998). A total of 98 days were spent observing the nests, with observation periods usually starting at 08:00 h and continuing until 18:00 h. Construction of each hide, at 20-40 m from the nest, took a few hours in total by three people. The work was spread over several days and was completed some days prior to hatching, in order to minimise disturbance to the birds. The young fledged from all four nests.

Observations were made with a ×30 telescope. All prey items delivered to the nest were identified to species on the basis of features described in Arnold & Ovenden (2002). Prey size was estimated to the nearest 10 cm and classified (snakes and European glass lizards) as belonging to one of six size classes (40-60 cm, 61-80 cm, 81-100 cm, 101-120 cm, 121-140 cm and 141-160 cm). Also, time of arrival with prey, proportion of prey item consumed by the eaglet and its parents, part of prey swallowed first and, when possible, the sex of the eagle delivering the prey were recorded.

Data analysis

We collected and captured 105 snakes, 21 glass lizards and 30 other lizards (65% fresh road kills), and measured total length and weight for each individual. Using these data, a linear regression function was made for each species separately (Table 1), in order to estimate the weight of prey carried to the nest.

Diet breadth (B_A) was calculated according to Levins's standardized diet breadth (Hurlbert, 1978) formula:

$$B_A = [(1 / \sum p_i^2) - 1] / (n - 1)$$

where p_i is the proportion of i^{th} prey in different categories and n is the number of prey categories. The value of B_A ranges between 0 and 1. If prey are equally proportional in each category then $B_A = 0$, whereas $B_A = 1$ when all prey occur in one category (Krebs, 1999).

Chi-square (χ^2) analysis was used to test for differences in frequency of different prey types among years, breeding stages, and diets of adults and young. However, when in some cases small samples did not meet test assumptions, prey categories were pooled.

All statistical analyses (χ^2, ANOVA, regression and Kruskal-Wallis tests) were carried out using Minitab statistical software (version 12), and SPSS (version 15.0), and differences were considered significant when $p \leq 0.05$.

RESULTS

Diet composition of young

A total of 116 prey deliveries were recorded at four nests. Since there were no differences in prey types carried to each of the four nests, the data were pooled and the occurrence and biomass for each species was estimated (Table 2). Overall, snakes and lizards predominated in the diet of the young. The ratio of these groups was similar among the nests (2×4 contingency test: $\chi^2 = 2.781$, df = 3, $p = 0.427$). Snakes represented nearly 80% of the prey by numbers and 89% of prey biomass. Snake prey included six species, with grass snakes contributing 45% to total prey occurrence and 29% to total prey biomass. Montpellier snakes were followed as numerically important prey, while large whip snakes followed in terms of prey biomass (Table 2). Lizard prey brought to the nests included three species. Green lizards represented 11.2% of prey items, whereas glass lizards accounted for 9% of prey biomass. Other prey species delivered to the nests were amphibians, young tortoises and small mammals, but of these only a common toad (*Bufo bufo*) was consumed.

Prey delivery rate

During 98 observation days at four nests, 111 prey deliveries were observed. In addition, five prey species were recorded at the nests having been delivered during the previous days. Short-toed eagles delivered one prey item day^{-1} in 82 observation days, two prey items day^{-1} in 13 observation days, three prey items day^{-1} in one observation day and 0 prey items day^{-1} in two observation days. The delivery rate was 1.1 prey item day^{-1}, and there were no differences in prey delivery rate (prey items day^{-1}) among the observed nests

TABLE 1. Relationships (W = aL + b) in snakes and glass lizard between total length (L in cm) and weight (W in g) in DLS NP in 1996-98

Species	***N***	**a**	**b**	**R^2**	**Pearson correlation**	
					r	***p*-values**
Natrix natrix	28	2.0276	–53.686	91.18	0.955	< 0.001
Natrix tessellata	23	3.3124	–83.346	92.38	0.961	< 0.001
Coluber caspius	30	5.1732	–244.29	81.80	0.904	< 0.001
Malpolon monspessulanus	13	3.4888	–125.17	86.17	0.928	< 0.001
Elaphe longissima	11	5.2415	–341.67	78.12	0.884	< 0.001
All snakes	105	4.1960	–149.92	87.78	0.937	< 0.001
Pseudopus apodus	21	6.7701	–250.96	75.37	0.868	< 0.001

TABLE 2. Food habits of young and adult short-toed eagles in the DLS NP in the breeding seasons of 1996-98. Chick diet based on visual observations during 98 days at 4 nests, and adult diet assessed by analysis of 167 pellets

Species	**Young diet**				**Adult diet**	
	Occurrence		Biomass		Occurrence	
	N	%	*g*	%	*N*	%
Snakes	**92**	**79.3**	**18,414.8**	**88.9**	**199**	**84.3**
Natrix natrix	52	44.8	6,007.7	29.0	103	43.6
N. tessellata	6	5.2	1,206.3	5.8	4	1.7
Coluber caspius	11	9.5	4,529.5	21.9	59	25.0
C. najadum	2	0.9	287.6	1.4	3	1.3
Malpolon monspessulanus	15	12.9	4,437.0	21.4	21	8.9
Elaphe longissima	5	4.3	1,698.6	8.2	9	3.8
Unknown	1	0.9	148.0	1.2	—	—
Lizards	**21**	**18.1**	**2,262.0**	**10.9**	**10**	**4.2**
Pseudopus apodus	7	6.0	1,865.0	9.0	6	2.5
Lacerta viridis	13	11.2	377.0	1.8	4	1.7
Podarcis erhardii	1	0.9	20.0	0.1	—	—
Amphibians	**1**	**0.9**	**31.0**	**0.1**	—	—
Bufo bufo	1	0.9	31.0	0.1	—	—
Tortoises	**1**	**0.9**	—	—	**9**	**3.8**
Testudo spp.	1	0.9	—	—	9	3.8
Mammals	**1**	**0.9**	—	—	**13**	**5.6**
Apodemus sylvaticus	1	0.9	—	—	4	1.7
A. agrarius	—	—	—	—	3	1.3
Microtus spp.	—	—	—	—	6	2.6
Birds	—	—	—	—	**2**	**0.9**
Turdus merula	—	—	—	—	2	0.9
Insects unidentified	—	—	—	—	**3**	**1.3**
Grand total	**116**	**100.0**	**20,707.7**	**100.0**	**236**	**100.0**
Dietary breadth (B_A)	0.253				0.184	

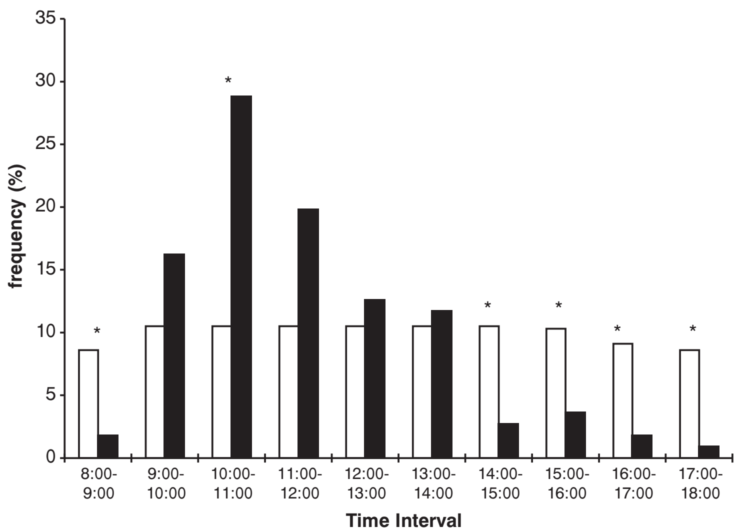

FIG. 1. Expected (open bars) and observed prey deliveries (hatched bars) to the nest by short-toed eagles during each of ten 1-h time intervals throughout the day ($n = 111$). Asterisks indicate a significant difference between observed and expected frequencies. Expected and observer proportions of prey delivered to the nest are calculated from the number of times spent during each of the ten time intervals watching a nest, and from the number of eagles arriving with food at the nest during each of the ten time intervals following the method of Neu *et al.* (1974).

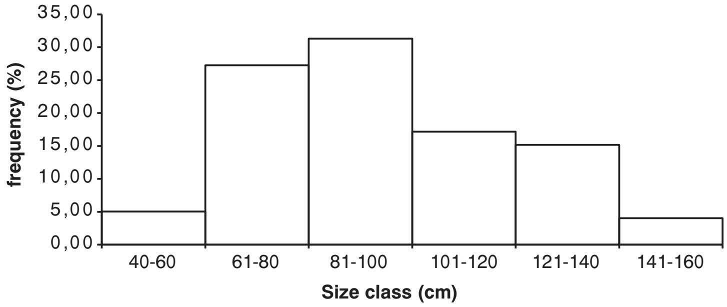

FIG. 2. Size class distribution of prey (snakes and European glass lizards) delivered to the nest ($n = 99$).

(one-way ANOVA: $F_{3,94} = 1.040$, $p = 0.379$). In addition, there were no significant differences in prey delivery rate among the seven ten-day age intervals of the growing nestlings (Kruskal-Wallis test: H = 10.934, df = 6, $p = 0.090$) (Table 3). The average prey weight delivered to the nest was 211.3 g day^{-1} (s.e. = 13.4 g day^{-1}) and there was no significant difference among the seven 10-day stages ($F_{6,91} = 1.73$, $p = 0.122$). However, there was some variation among the seven stages in the mean weight delivered to the nest. For example, heavier prey items were delivered each day when the young bird was between 31 and 40 days old in relation to others stages. Most (78%) of the prey deliveries occurred between 09.00 and 12.00 h, with a peak between 10.00 and 11.00 h. Observed deliveries were not distributed randomly across the day ($\chi^2 = 32.280$, df = 9, $p < 0.001$) (Fig. 1).

The prey-size distribution delivered to the four nests during 1996-1998, is shown in Figure 2. Overall, there was a significantly greater (75.75%) proportion of medium size (61-120 cm) prey delivered to the nest ($\chi^2 = 19.350$, df = 5, $p = 0.002$). In addition, there was an avoidance of small size prey (< 60 cm in length) and large size prey (> 140 cm in length) by the short-toed eagles.

Prey consumption and feeding behaviour

Of 116 prey delivered to the nest, 69% were eaten whole, 29% were eaten partially and the rest were not consumed by the young. Most of the snakes and European glass lizards (81.9%) were eaten head first and 18.1% were eaten tail first. As the young grew larger, few snakes were swallowed tail first (2×3 contingency test: $\chi^2 = 7.542$, df = 2, $p = 0.023$).

TABLE 3. Prey items brought to short-toed eagle nests and prey consumed by the young during seven 10-day stages of development of the chick, in the DLS NP in 1996-98. N = number of observation days during each of the seven age categories

		Prey carried to the nest				Prey consumed by the young				% Prey consumed/carried
Young age (days)	N	Deliveries	Delivery rate (items day^{-1})	Total weight [d] (g)	Mean weight (g day^{-1})	Whole	Part	Total weight (g)	Mean weight (g day^{-1})	
0-10	14	14 [a]	1.000	2,276.0	162.6	0	14	317.1	22.7	13.93
11-20	14	15 [b]	1.071	2,291.9	163.7	4	13	1,123.9	80.3	49.04
21-30	14	16 [c]	1.143	2,657.9	189.9	13	4	2,471.7	176.6	92.99
31-40	13	18	1.385	3,741.2	287.8	17	1	3,571.5	274.7	95.46
41-50	14	18	1.286	3,485.3	249.0	16	2	3,385.0	241.8	97.12
51-60	15	17	1.133	3,470.5	231.4	17	0	3,470.5	231.4	100.00
> 60	14	13	0.929	2,785.7	199.0	13	0	2,785.7	199.0	100.00

[a] One *Apodemus sylvaticus* and one *Testudo* sp. found on nest but not eaten
[b] One *Elaphe longissima* and *Coluber caspius* found on nest and eaten by chick
[c] One *Natrix natrix* found on nest and eaten by chick
[d] Weights of snakes and glass lizards were estimated from their regression curve (Table 1), except for *Columber najadum* which was estimated from the combined snake species regression curve. Weight of *Lacerta viridis* was 29 g ($n = 21$), and of *Podarcis erhardii* 19.78 g (n = 9)

The overall mean weight consumed per day by a nestling short-toed eagle was 174.8 g day^{-1} (s.e. = 14.0 g day^{-1}), with significant differences among the seven ten-day periods of the nestling cycle ($F_{6,91} = 9.04$, $p < 0.001$) (Table 3). The percentage of food consumed by the young, increased from 14% during the first ten days of age, to 93% when the young were 21-30 days old, and to 100% from age 51 days old onwards. Food not consumed by the chick was swallowed by the female, and consequently her share declined from 86% to 0% as the young grew older. The young started to eat whole prey items from the end of the second 10-day period.

Diet of adults

Only nine prey remains were collected during the study period, constituting three grass snakes, one large whip snake, one Montpellier snake, three glass lizards, and one tortoise *Testudo* spp. two years old. As the sample of prey remains was so small, these items were excluded from the diet analysis.

Out of a total of 167 pellets analysed, 101 were found to contain a single species, 63 were composed of two species and 3 were composed of three species. A total of 236 prey items were identified in 167 pellets. The most numerous prey items were snakes, constituting 84% of the diet (Table 2). Of the prey identified in pellets, grass snakes and large whip snakes were the most abundant, comprising over 80% of the snakes. If the data are split into *Natrix* spp. and non-*Natrix* spp., there was a significant difference among nine nests from which more than 12 pellets were collected from each one during the three years of the study ($\chi^2 = 21.93$, df = 8, $p = 0.005$). The contribution of *Natrix* spp. in the diet declined with distance of the nest from the nearest water concentration during the summer ($r = -0.911$, $p = 0.001$). The nests in the vicinity of open areas (including cultivated areas, grasslands and rocky areas) were associated with a high proportion of *Natrix* spp. in the diet nests ($r = 0.758$, $p = 0.018$).

Lizards and tortoises were found in similar proportions in the short-toed eagle diet (4.2% and 3.8%, respectively). Remains of small mammals, birds and insects were found in combination with scales of snakes, their main predators. It was not possible to determine whether these prey items were captured by the snakes or directly by the eagles. Miscellaneous prey items were mostly found during the post-fledging stage and incubation.

In order to make comparisons between adult and young short-toed eagle diets, data from pellets and remains were pooled because there were no significant differences between both sets of data (for three groups of prey: snakes, lizards and tortoises) either among the three study years, or among the breeding stages (incubation, brooding and post-fledging periods) ($\chi^2 = 7.048$, df = 4, $p = 0.134$; $\chi^2 = 4.524$, df = 4, $p = 0.340$, respectively). There was a significant difference between the diets of adult and nestling short-toed eagles with respect to the proportions of reptiles and other prey items ($\chi^2 = 24.37$, df = 3, $p < 0.001$) (Fig. 3). This was mainly due to a smaller proportion of lizards and a higher proportion of miscellaneous prey items found in pellets than observed being brought to the nests. When snakes and glass lizards were grouped as large prey up to 2 m in length (large whip snakes, Montpellier snakes and Aesculapian snakes) and as medium prey up to 1 m in length (grass snakes, dice snakes, Dahl's whip snakes and European glass lizards), there was a significant difference be-

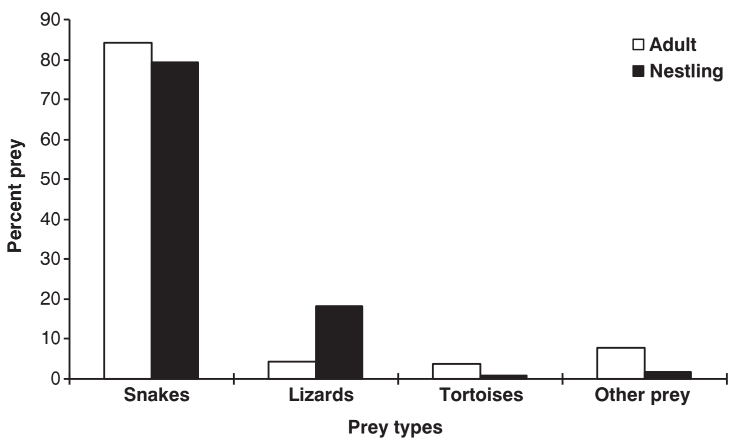

FIG. 3. Frequency of prey types identified from pellets (adult diet) and observed being carried to the nests (nestling diet) of short-toed eagles in the DLS NP in 1996-1998.

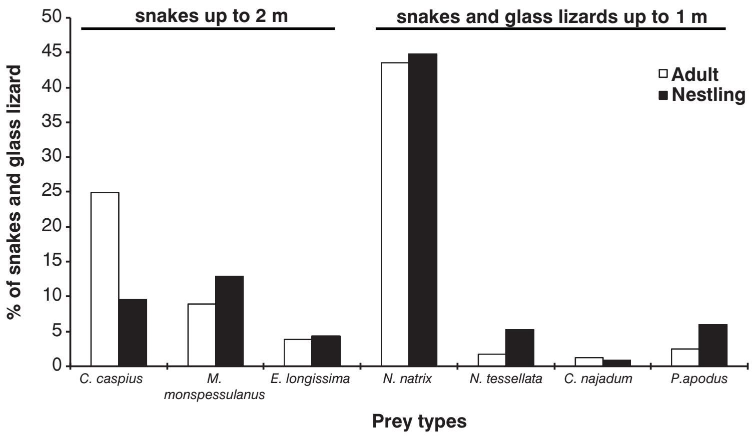

FIG. 4. Frequency (%) of snake species and glass lizards found in pellets (adult diet) and those observed being delivered to the nests (nestling diet) of short-toed eagles in the DLS NP in 1996-98. Data grouped according to the length of each species.

tween prey size found in pellets and via direct observations at nests ($\chi^2 = 16.848$, df = 6, $p = 0.01$) (Fig. 4). Overall, the proportion of large-sized snakes was higher in pellets (43%) than in direct observations (31%), while the proportion of medium-sized snakes and glass lizards was higher in direct observations (69%) than in pellets (57%).

The values of diet breadth (Table 2) showed that adult short-toed eagles had a relatively broader diet than young eagles.

DISCUSSION

Diet composition

The present study identifies that the short-toed eagle can be regarded as a specialist predator in snakes. This finding was confirmed from dietary breadth analysis, and it was also suggested by other authors (Boudoint *et al.*, 1953; Thiollay, 1968; Becsy, 1971; Amores & Franco, 1981; Jaksic & Delibes, 1987; Petretti, 1988; Vlachos & Papageorgiou, 1994; Bakaloudis *et al*., 1998; Gil & Pleguezuelos, 2001; Moreno-Rueda & Pizarro, 2007). Short-toed eagles in the study area specialised in consuming mainly grass snakes, Montpellier snakes and large whip snakes, both in terms of numerical percentage and biomass. Other reptilian prey found in the diet included green lizard, European glass lizard, Erhard's wall lizard and tortoises (*Testudo* spp.). However, some variation in the number of lizards in the diet of short-toed eagles was found between adults and nestlings. Differences in food assessment techniques in the present study may have been responsible for some of the variation recorded in the eagles' diet (Marti *et al*., 2007). For example, lizards were recorded less frequently in the diet of adult short-toed eagles than in the nestlings' diet. This could be accounted for if lizard scales are more digestable than snake scales and hence have a lower probability of occurring in pellets or, conversely, that smaller prey was brought to the nest when nestling was still small.

The short-toed eagles preyed mainly on medium-sized snakes around 1 m in length, including *Natrix* species, Dahl's whip snake and European glass lizard (Figs 2 and 4). Similar prey sizes have been reported by Madon (1993) and Gil & Pleguezuelos (2001), both of whom analysed the diet of short-toed eagles during the breeding season, whereas Petretti (1988) noted that snakes taken in his study area measured from 60 cm to 100 cm in length. The likely preference of specific-sized prey during the breeding season may be associated with the optimization of energy and time budgets of the short-toed eagles. Large-sized prey (more than 1 m in length) may need more handling time. On the other hand, small-sized prey (less than 60 cm in length) may provide less energy than the eagles required. The present study shows that short-toed eagles do not avoid taking venomous snakes, such as Montpellier snakes. However, other venomous snakes, such as nose-horned viper, are probably avoided due to their small size (usually less than 65 cm in length; Arnold & Ovenden, 2002). Differences in size contribution of snakes between the adult and nestling short-toed eagle diet were probably reflecting differences in the sampling procedures used and the nests selected for study.

Of the reptilian prey identified in the short-toed eagle's diet in the present study, 72% (8 of 11 species) were associated with open habitat types, such as intensively and extensively cultivated fields, grasslands or degraded oak forests (Bakaloudis *et al*., 1998; Arnold & Ovenden, 2002; Petrov, 2004; Kati *et al*., 2007).

Open habitat types, where snakes and lizards are more susceptible to capture, are foraging sites preferred by short-toed eagles (Thiollay, 1968; Choussy, 1973; Petretti, 1988; Bocca, 1989; Moreno-Rueda & Pizarro, 2007; Bakaloudis, 2009), as well as by other raptors (e.g. long-legged buzzard *Buteo rufinus*, Alivizatos & Goutner, 1997; Bonelli's eagle *Aquila fasciata*, Ontiveros *et al.*, 2005).

The proportion of non-reptilian prey (rodents, birds and insects) was higher in adult than in nestling diets. Most of the rodents found in pellets are nocturnal and occur in habitat types similar to those of their predators (McDonald & Barrett, 1993). They may have been eaten by snakes rather than captured by the eagles. If this is true, and short-toed eagles do not normally capture rodents, birds and insects, the results of our study concur with those reported by Boudoint *et al.* (1953), Becsy (1971), Choussy (1973), Amores & Franco (1981), despite the fact that most of these studies relied on direct observations at the nest. On the other hand, it has been suggested that short-toed eagles feed on non-reptilian prey during adverse weather when reptiles are less active (Thiollay, 1968; Petretti, 1988; Ivanovsky, 1992; Varga & Rekasi, 1993; Vlachos & Papageorgiou, 1994). In our study area, most of the miscellaneous prey items were found during April and May (incubation), and August and September (post-fledging), when the weather is more unpredictable with rainy periods. Thus, more information on eagle hunting behaviour is needed to clarify the importance of non-reptilian prey in the short-toed eagle diet.

The present study added tortoises to the diet of European short-toed eagles. Carapace scutes from young tortoises were found in pellets at different nests. Most of the tortoises appeared in the diet during the nestling and post-fledging stages. Hermann's tortoise and spur-thighed tortoise both reach very high densities in cultivated areas and in openings in the forest (Helmer & Scholte, 1985; Petrov, 2004), where short-toed eagles were frequently observed foraging for food (Bakaloudis, 2009).

Feeding rates, food consumption and feeding behaviour

Perrins (1965) suggested that birds attain higher nesting success and better survival of young when hatching dates are closer to the peak of food availability. Similarly, many raptors fit their breeding period around maximum prey abundance (Newton, 1979). In the study area, short-toed eagles arrive with the appearance of reptiles early in April, and the hatching period, from late May to early June (Bakaloudis *et al.*, 2005), coincides with higher snake availability (Bakaloudis *et al.*, 1998). Prey carried to the nest reflects the nestlings' diet and consists mainly of snakes (79.3% by numbers and 88.9% by biomass). The young short-toed eagle's diet, as determined by direct observations at four nests, is in agreement with earlier findings in France (Boudoint *et al.*, 1953; Choussy, 1973), Hungary (Becsy, 1971) and Italy (Petretti, 1988). Colubrids (grass snake, dice snake, Montpellier snake, large whip snake, Dahl's whip snake and Aesculapian snake) were the most important prey items that were delivered to the nest and they comprised the principal food for the young.

The delivery rate of the short-toed eagle throughout the nestling period averaged 1.1 prey items per day. The rate of prey delivery did not vary significantly during the nestling period as with certain other raptors (osprey *Pandion haliaetus*: Green 1976; sparrowhawk *Accipiter nisus*: Geer, 1981; golden eagle: Collopy, 1984; kestrel *Falco tinnunculus*: Village, 1990; prairie falcon *Falco mexicanus*: Holthuijzen, 1990). The prey delivery rate was approximately 1 prey item per day during the first 20 days after hatching, increasing to about 1.4 prey items per day during the fourth ten-day growth period, and decreasing steadily to below 1 prey item per day during the late period of brooding before the young left the nest. During the first 20 days after hatching, the male short-toed eagles delivered all the prey, while the females shaded, brooded and fed the young. During the third ten-day growth stage of the young (21-30 days old), its plumage started to appear and the delivery rate by males increased to 1.143 prey items per day. At this time the females began spending more time away from the nest, especially from those nests which were shaded from above. The prey delivery rate peaked at 1.385 and 1.286 prey items per day during the fourth and fifth ten-day growth periods, respectively. Although the females contributed to this increase, most of the deliveries were made by the males. Prey delivery rate decreased from 1.133 prey items per day during the sixth growth stage of the young, to 0.929 prey items per day during the last growth stage. Reduced prey deliveries during the late period of brooding have been observed in other eagles (Collopy, 1984), and this reduction has been suggested as a mechanism facilitating the fledging process of the young (Brown, 1955).

Although the delivery rate (1.1 prey items per day) in the present study was lower than that observed in Italy (1.8 prey items per day) by Petretti (1988), the estimated weight of prey delivered to nests averaged 211.3 g day^{-1} (Table 3), slightly more than the 194 g day^{-1} in Italy (Petretti, 1988). This difference may have partly resulted from the methods to estimate prey weight in the two studies or, more likely, from the eagles' captured heavier prey in our study area. In the present study, the weight of each species was calculated separately from its linear regression function (Table 1), while Petretti (1988) estimated the weight of all species brought to nests from a function based on just two colubrids. Most of the species delivered to nests measured from 60 to 120 cm in length, weighing between 68 to 376 g per individual. Occasionally a few large whip snakes (150 cm long) with an estimated weight of 532 g per individual were brought to nests. The findings of our study concur with those reported by Amores & Franco (1981) in Spain where prey weight ranged from 120 to 240 g. In Italy, Petretti (1988) found that the preferred prey delivered to nests ranged from 73 to 127 g per individual. Apparently, our short-toed eagles meet the food requirements of chicks by bringing fewer, but heavier, prey items, the latter being more abundant in northeastern Greece than in Italy (Petretti, 1988).

Short-toed eagles carried a higher proportion of medium-sized snakes and glass lizards to nests compared to what they ate themselves (Fig. 4). The principal prey for the young were *Natrix* spp. up to 1 m in length. The nests were generally close to water and the surrounding area had a high proportion of open habitats. According to the central-place foraging theory, where size of captured prey should increase with increasing travel distance (Orians & Pearson, 1979), this difference might indicate that short-toed eagles hunt near their nests in order to deliver the medium-sized prey to their nests, while they hunt over greater distances to find larger prey for themselves. Another possible explanation for the different proportions of large size prey in the diet of adult and young short-toed eagles is that some pellets were probably from the females. Although the short-toed eagle is not a strongly dimorphic species (3 species of snake eagles have a mean dimorphism of 1.03; Schantz & Nilsson, 1981) as are other Accipiters (22 species of Accipiters have a mean dimorphism of 1.07; Schantz & Nilsson, 1981), the female is slightly larger than the male (mean weight of male: 1,664 g; mean weight of female: 1,735 g; Cramp & Simmons, 1980). Consequently, the larger female could possibly exploit larger prey than the male or young, which in turn accounts for the scales of large prey species appearing in the pellets.

The female resumed hunting before the young left the nest, and contributed to prey delivery during the later stages of the nestling cycle. Food consumption increased as the nestling grew older. On average, the nestling consumed 174.8 g day^{-1}, increasing from 10 g day^{-1} during the first days after hatching to 530 g day^{-1} during the later stages of growth. Daily food consumption peaked between 31 and 40 days of age. Petretti (1988) estimated that a nestling short-toed eagle consumed on average 157 g day^{-1} over the nestling period (30-215 g day^{-1}), and Boudoint *et al.* (1953) 120-125 g day^{-1}. The female remained close to the nest during incubation, and the early stages of the nestling period (brooding, shading, feeding). The young occasionally began to feed just before 20 days of age. As the nestling grew, the female spent less time on the nest. Although the female usually stopped feeding her young after the third growth stage in the three nests observed in 1996 and 1997, in the nest observed during 1998, the female continued to feed her young until the fifth stage of growth (41-50 days old).

Most of the short-toed eagle deliveries occurred between 09:00 and 12:00 h, exhibiting a unimodal pattern of prey delivery (Fig. 1). Petretti (1988) found a similar diurnal rhythm of deliveries (from 09:00 to 13:00 h). Reptiles reduce their activity during the warmer midday hours, showing highest activity in the morning and –to a smaller extent– during late afternoon (Taylor, 1998; Bakaloudis, 2000). Consequently, short-toed eagle's hunting activity corresponds with the activity pattern of their main prey species (Bakaloudis *et al*., 1998; Bakaloudis, 2009).

In conclusion, the short-toed eagle has a specialised diet on reptilian prey species and appears to forage selectively for certain sizes. Selection of different-sized reptilian prey during the breeding season may be due to different energy requirements of nestling and adult eagles, or due to biases produced by the different diet-analysis techniques. Although its morphological adaptations provide protection from venomous snake-bite, in our study venomous snakes were not taken frequently probably, due to their small sizes. Parents have a distinctive behaviour during the nestling stage, with male to contribute more in the delivery food to the nest and female to care for the chick. The observed heavier prey delivered to the nests may be attributed by the high abundance of prey species in our study area, which in turn positively affect the high overall breeding success of the short-toed eagle in the region (Bakaloudis *et al*., 2005). Future monitoring of the interaction between short-toed eagles and their reptilian prey could help us to better understand the role of reptiles in the eagle's feeding ecology.

ACKNOWLEDGEMENTS

D.E.B. was financially supported by '*Sofia Chlorou*' Legacy from the National Technical University of Athens NTUA (National Metsovion Polytechnic). We are very grateful to Dr G.J. Holloway for his help in various parts of this study. We are particularly grateful to Professor Richard Sibly and Professor Steven Redpath who improved critically the original manuscript. We also thank Drs R. Bijlsma and G. Moreno-Rueda for their insightful suggestions on the first version of the manuscript, and two anonymous reviewers for their comments on the manuscript.

REFERENCES

Alivizatos H, Goutner V, 1997. Feeding habits of the long-legged Buzzard (*Buteo rufinus*) during breeding in north-eastern Greece. *Israel Journal of Zoology*, 43: 257-266.

Amores F, Franco A, 1981. Alimentation et écologie du Circaète Jean-le-Blanc dans le sud de l'Espagne. *Alauda*, 49: 59-64.

Arnold EN, Ovenden D, 2002. *Reptiles and amphibians of Europe*. Princeton University Press, Princeton, New Jersey.

Bakaloudis DE, 2000. *The ecology of Short-toed Eagle (Circaetus gallicus, Gm.) in Dadia-Lefkimi-Soufli forest complex, Thrace, Greece*. Ph.D. Thesis, University of Reading, England.

Bakaloudis DE, 2009. Implications for conservation of foraging sites selected by Short-toed Eagles (*Circaetus gallicus*) in Greece. *Ornis Fennica*, 86: 89-96.

Bakaloudis DE, Vlachos CG, Holloway GJ, 1998. Habitat use by short-toed eagles *Circaetus gallicus* and their reptilian prey during the breeding season in Dadia Forest (north-eastern Greece). *Journal of Applied Ecology*, 35: 821-828.

Bakaloudis DE, Vlachos CG, Holloway GJ, 2000. Nest features and nest-tree characteristics of Short-toed Eagles (*Circaetus gallicus*) in the Dadia-Lefkimi-Soufli forest, northeastern Greece. *Journal of Raptor Research*, 34: 293-298.

Bakaloudis DE, Vlachos CG, Papageorgiou N, Holloway GJ, 2001. Nest-site habitat selected by Short-toed Eagles *Circaetus gallicus* in Dadia Forest (north-eastern Greece). *Ibis*, 143: 391-401.

Bakaloudis DE, Vlachos CG, Holloway GJ, 2005. Nest spacing and breeding performance in Short-toed Eagle *Circaetus gallicus* in northeast Greece. *Bird Study*, 52: 330-338.

Becsy L, 1971. Data on the food of the Short-toed Eagle (*Circaetus gallicus*). *Allattani Kozlemenyek*, 58: 166.

Bocca M, 1989. Status del Biancone (*Circaetus gallicus*), dell'Aquila reale (*Aquila chrysaetos*) e del Pellegrino (*Falco peregrinus*) in Valle d'Aosta. *Bollettino Museo Regionale di Scienze Naturali di Torino*, 7: 163-183.

Boudoint Y, Brosset A, Bureau L, Guichard G, Mayaud N, 1953. Etude de la biologie du Circaète Jean-le-Blanc. *Alauda*, 21: 86-112.

Brown LH, 1955. Supplementary notes on the biology of the large birds of prey of Embu District, Kenya Colony. *Ibis*, 97: 38-64.

Choussy D, 1973. Observations sur le Circaète Jean-le-Blanc. *Nos Oiseaux*, 32: 82-89.

Collopy MW, 1984. Parental care and feeding ecology of Golden Eagle nestlings. *Auk*, 101: 753-760.

Cramp S, Simmons KEL, 1980. *The birds of the western Palearctic, Vol. 2*. Oxford University Press, Oxford.

Geer T, 1981. Factors affecting the delivery of prey to nestling Sparrowhawks (*Accipiter nisus*). *Journal of Zoology (London)*, 195: 71-80.

Gil JM, Pleguezuelos JM, 2001. Prey and prey-size selection by the short-toed eagle (*Circaetus gallicus*) during the breeding season in Granada (south-eastern Spain). *Journal of Zoology (London)*, 255: 131-137.

Green R, 1976. Breeding behaviour of Ospreys *Pandion haliaetus* in Scotland. *Ibis*, 118: 475-490.

Helmer W, Scholte P, 1985. *Herpetological research in Evros, Greece: proposal for a biogenetic reserve*. Societas Europaea Herpetologica. Research Institute of Nature Management of Arnhem and Department of Animal Ecology of Nijmegen.

Holthuijzen AMA, 1990. Prey delivery, caching, and retrieval rates in nesting Prairie Falcons. *Condor*, 92: 475-484.

Hurlbert SH, 1978. The measurement of niche overlap and some relatives. *Ecology*, 59: 67-77.

Ivanovsky VV, 1992. Ecology of short-toed eagle nesting in the Byelorussian Poozerje. In: Kurochkin EN, ed. *Modern ornithology.* Nauka Publishers, Moscow: 69-77 (in Russian).

Jaksic FM, Delibes M, 1987. A comparative analysis of food-niche relationships and trophic guild structure in two assemblages of vertebrate predators differing in species richness: causes, correlations, and consequences. *Oecologia*, 71: 461-472.

Kati V, Foufopoulos J, Ioannidis Y, Papaioannou H, Poirazidis K, Lebrun P, 2007. Diversity, ecological structure and conservation of herpetofauna in a Mediterranean area (Dadia National Park, Greece). *Amphibia-Reptilia*, 28: 517-529.

Krebs CJ, 1999. *Ecological methodology*. 2[nd] *edn*. Benjamin/

Cummings, Menlo Park, California.

Madon P, 1993. *Les rapaces d'Europe*. Toulon, France.

Marti CD, Bechard M, Jaksic FM, 2007. Food habits. In: Bird DM, Bildstein KL, eds. *Raptor research and management techniques*. Hancock House Publishers: 129-152.

McDonald DW, Barrett P, 1993. *Mammals of Britain and Europe*. Harper Collins, London.

Moreno-Rueda G, Pizarro M, 2007. Snake species richness and shrubland correlate with the short-toed eagle (*Circaetus gallicus*) distribution in south-eastern Spain. *Annales Zoologici Fennici*, 44: 314-320.

Neu CW, Byers CR, Peek JM, 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management*, 38: 541-545.

Newton I, 1979. *Population ecology of raptors*. Poyser, Berkhamstead, UK.

Ontiveros D, Pleguezuelos JM, Caro J, 2005. Prey density, prey detectability and food habits: the case of Bonelli's eagle and the conservation measures. *Biological Conservation*, 123: 19-25.

Orians GH, Pearson NE, 1979. On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR, eds. *Analysis of ecological systems*. Ohio State University Press, Columbus: 155-177.

Papageorgiou N, Vlachos C, Sfougaris A, 1991. *Identification of mammals by hair morphology.* University Studio Press, Thessaloniki (in Greek).

Papageorgiou N, Vlachos C, Sfougaris A, Bakaloudis D, 1993. *Identification of reptiles by scale morphology*. University Studio Press, Thessaloniki (in Greek).

Perrins CM, 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. *Journal of Animal Ecology*, 34: 601-647.

Petretti F, 1988. Notes on the behaviour and ecology of the Short-toed Eagle in Italy. *Gerfaut*, 78: 261-286.

Petrov BP, 2004. The herpetofauna (Amphibia and Reptilia) of the eastern Rhodopes (Bulgaria and Greece). In: Beron P, Popov A, eds. *Biodiversity of Bulgaria. 2. Biodiversity of Eastern Rhodopes (Bulgaria and Greece)*. Pensoft & National Museum of Natural History, Sofia: 863-879.

Preston CR, 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure. *Condor*, 92: 107-112.

Reichholf J von, 1988. The Short-toed Eagle (*Circaetus gallicus*) in Bavaria: A rare but regular migrant along the northern Fringe of the Alps. *Anzeiger der Ornithologischen Gesellschaft in Bayern*, 27: 115-124.

Rosenberg KV, Cooper RJ, 1990. Approaches to avian diet analysis. *Studies in Avian Biology*, 13: 80-90.

Schantz T von, Nilsson IN, 1981. The reversed size dimorphism in birds of prey: a new hypothesis. *Oikos*, 36: 129-132.

Taylor RC, 1998. *Diurnal activity and individual range behaviour in reptiles of the Dadia forest reserve, North-eastern Greece*. M.Sc. Dissertation, University of Reading, England.

Thiollay JM, 1968. Essai sur les rapaces du midi de la France: distribution-ecologie. Circaète Jean-le-Blanc (*Circaetus gallicus*). *Alauda*, 336: 179-189.

Varga Z, Rekasi J, 1993. Food and population dynamics of birds of prey. *Aquila*, 100: 123-136.

Village A, 1990. *The kestrel*. Poyser, London.

Vlachos CG, Papageorgiou NK, 1994. Diet, breeding success, and nest-site selection of the short-toed eagle (*Circaetus gallicus*) in northeastern Greece. *Journal of Raptor Research*, 28: 39-42.