

Nest spacing and breeding performance in Short-toed Eagle *Circaetus gallicus* in northeast Greece

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Capsule There is some evidence of susceptibility to stochastic or human factors.

Aims To describe the phenology and breeding success of one of the densest populations of Short-toed Eagle in Europe.

Methods All nests in the Dadia–Lefkimi–Soufli forest in northeast Greece were located and visited regularly throughout the 1996–98 breeding seasons. Data on every stage of the breeding cycle were collected and related to among-year variation in the weather conditions during March to June.

Results A total of 58 pairs were located during the three-year study spread across 22 territories (the same territories are usually occupied each year). The nests were evenly spaced (mean of 2.7 km between nests). Adults arrived between mid-March and mid-April. Only one egg per nest was laid. Nestlings fledged on average after 68.9 days. Eagles departed between 8 September and 2 October.

Conclusions Arrival date determines laying date. The population size appears to be stable but the species has a relatively low reproductive rate and takes three to four years to mature, consequently it may be susceptible to stochastic or human-mediated factors.

It has been well documented that the breeding density of raptors can be limited by nest-site availability and food supply in some species (Newton 1979). Also, regional variations in raptor breeding density may occur within their normal breeding range and where nesting sites are available these density differences may be influenced by the food supply, which often varies according to soil productivity (Newton 1979, Newton *et al.* 1986). However, some raptor breeding populations also fluctuate in response to inclement weather before the breeding cycle, e.g. Kestrel *Falco tinnunculus* (Kostrzewa & Kostrzewa 1990, 1991), or during the breeding cycle, e.g. Honey Buzzard *Pernis apivorus* (Kostrzewa 1989). Recently, weather conditions have been more widely recognized as important factors affecting some raptor's breeding performance and success by affecting either their prey abundance and behaviour or their hunting efficiency. Inclement weather can also directly influence breeding success by killing adults and young or by chilling the embryo. Sparrowhawk *Accipiter nisus* laying dates are later in the

breeding season when weather conditions are bad (Newton & Marquiss 1986) whereas reproductive success of many raptors can be adversely affected by rainfall during the breeding season, e.g. Kestrel (Village 1986, Kostrzewa & Kostrzewa 1990), Peregrine Falcon *Falco peregrinus* (Mearns & Newton 1988, Olsen & Olsen 1989), Honey Buzzard (Kostrzewa 1989), Buzzard *Buteo buteo*, Goshawk *Accipiter gentilis* and Golden Eagle *Aquila chrysaetos* (Steenhof *et al.* 1997).

Although the Short-toed Eagle *Circaetus gallicus* (Gmelin 1788) was distributed widely across Europe, it has suffered a steep decline in numbers and range during the 19th and 20th centuries, and its distribution has become largely restricted to southern and eastern Europe (Cramp & Simmons 1980, Tucker & Heath 1994). Numerous estimates of breeding density have been made (Amores & Franco 1981, Cheylan 1981, Petretti 1988, Bocca 1989, Vlachos & Papageorgiou 1994). A few studies have also considered breeding success (Petretti 1988, Vlachos & Papageorgiou 1994). However, factors that may influence Short-toed Eagle breeding success, such as weather, have not received any attention.

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As a migratory species that depends on ectothermic prey (mainly snakes and lizards), its arrival in and departure from the study area correlate closely with the appearance and disappearance of available reptiles. Variations in the timing of movements of raptors to and from breeding areas are probably therefore influenced by both 'ultimate' (such as food supply) and 'proximate' (e.g. day length) factors (Newton 1979).

Here we aim to (1) estimate the breeding density and dispersion of nests, (2) present the timing of breeding and success, and (3) consider relationships between weather conditions and breeding parameters of Short-toed Eagles in the Dadia–Lefkimi–Soufli forest complex.

STUDY AREA AND METHODS

Study area

The Dadia–Lefkimi–Soufli (D-L-S) forest complex is located in the central part of Evros Province, northeast Greece (40°59'–41°15'N, 26°19'–26°36'E) and is characterized by rolling relief with low hills ranging from 20 to 700 m asl. The climate is sub-Mediterranean with mean summer temperatures of about 24°C. The minimum and maximum mean monthly temperatures in July are 15.3°C and 30°C, respectively, but daytime absolute maxima often exceed 39°C. A typical climatic feature of the study area is the large discrepancy between night and day temperatures (often >20°C). This may cause late frost in spring (usually in April) and early frost in autumn (usually in October). The mean annual precipitation is about 664 mm (ranging from 383.2 mm in 1992 to 1177.8 mm in 1980). Precipitation is concentrated in the cold season from autumn to spring, whilst the summer is dry and lasts from mid-June to the end of September. Northerly winds predominate during the year following the north–south aspect of Evros valley (Flokas 1992). Climatic data were obtained for the study area from the Hellenic National Meteorological Service and collected at the Soufli meteorological station located within the study area (15 m asl) for the last 25 years.

The study area is a mosaic of agricultural land, grasslands, shrublands, rocky areas, pine forests, oak forests, degraded oak forests, and mixed oak–pine forests. Vegetation and land use patterns of the D-L-S forest complex were described by Bakaloudis *et al.* (1998). Of the 37 156 ha of the study area, approximately 19.5% (7250 ha) of the forest complex consists of two cores established as protected areas for birds of prey in 1980.

Data collection

Short-toed Eagle territories in the study area from 1996 to 1998 were located using (a) historical descriptions of traditional nesting sites, (b) territorial behaviour of breeding pairs noted from high vantage points and (c) extensive exploratory surveys on foot (Fuller & Mosher 1987). Each year in the early and late breeding season all territories were visited every four or five days to record when Short-toed Eagles arrived (and established pairs) and departed from their nesting areas, respectively. Arrival and departure date was determined as the mid-date between two consecutive visits. In addition, in the early breeding season (between arrival from the winter quarters and laying date), pairs were located by observing their very obvious aerial and territorial behaviour, such as copulating, displaying, conflicts between neighbours and nest material deliveries, making it unlikely that any pairs were overlooked. The laying date was estimated by observing the male flying alone over the nesting territory or delivering food to the incubating female. Each nest was visited every two or three days during the late incubation period to record the hatching date. Where precise hatching date was unknown, it was calculated by back-dating from the date that the egg hatched with an error of ± 2 days (assuming 47 days for incubation; Boudoint 1953, Newton 1979). Each nest was also visited every 10–15 days during the brooding period to record any failure. All nests were visited every one or two days in the late brooding period to accurately record the fledging date and success. In order to minimize any potential disturbance, nests were monitored mainly over long distances during incubation, the first days after hatching and the last days before fledging using binoculars (10 × 40) or a telescope (60×) and avoiding days of inclement weather.

All nests were plotted on 1:5000 and 1:20 000 scale topographic maps and for each year nearest distances were measured to assess the mean nearest neighbour distance between neighbouring territories. For all years combined for each territory (i.e. 22 territories), the central point of the nest cluster was used to measure nearest neighbour distance for pairs that change nest from year to year (Dare & Barry 1990).

Unsuccessful breeding pairs were defined as those constructing or repairing a nest and laying an egg, but then failing during the breeding stages (incubation, hatching, brooding) before fledging; where possible, the reason for failure was recorded. Successful breeding pairs were defined as those successfully fledging a young

eagle (Newton 1979). However, it was unreliable to assume that a pair for which a nest had not been found was a non-breeding pair, especially in inaccessible areas. Mean brood size at hatching or hatching success (given as percentage) was defined as the total number of eggs hatching divided by the number of eggs laid (each pair laid a single egg). Fledging success (given as percentage) was defined as the total number of young fledging divided by the number of eggs hatching. Mean brood size at fledging or breeding success (given as percentage) was defined as the total number of young fledging divided by the number of eggs laid.

Density (km² per pair) was calculated by including all territorial pairs observed during early spring, whereas mean nearest neighbour distance, dispersion and reproduction were estimated from the number of known breeding pairs (successful and unsuccessful). In the study area, 22 Short-toed Eagle territories were located, and each year more than 86% of nests were found (1996: 94%, 1997: 86%, 1998: 90%).

Minimum (at 06:00 hours) and maximum (at 18:00 hours) daily temperature and precipitation (>0.2 mm) were used to calculate mean monthly temperature (mean of minimum and maximum) for May, and totals for precipitation and number of rain days for April, May and June.

Statistical analysis

The mean nearest neighbour distance (MNND) of Short-toed Eagle nests between years was analysed with one-way analysis of variance (ANOVA). All distances were log-transformed [$\log(x + 1)$] prior to statistical analysis to normalize variance. In order to test the nest dispersion pattern of Short-toed Eagles, the G statistic (the ratio of the geometric mean to the arithmetic mean of the squared distances) was used to estimate regularity or randomness (Brown 1975, Ripley 1979).^a

Breeding variables (arrival date, laying date, hatching date, fledging date, departure date, pre-laying period, brooding period and pre-migratory period) were tested for homoscedasticity and normality using Bartlett's test and Anderson–Darling test, respectively (Zar 1996). Heteroscedastic or non-normal variables were log-transformed [$\log(x + 1)$] prior to analysis. ANOVA (for normally distributed variables) or Kruskal–Wallis test (for non-normally distributed variables after transformation) was used to compare differences in breeding variables among years.

G-test of independence for 2 × 3 contingency tables was used to compare breeding parameters (hatching

success, fledging success and breeding success) among years and ANOVA was used to compare mean productivity at hatching and fledging stage among years (Zar 1996, Sokal & Rohlf 1995). All statistical analyses were performed using the SPSS (version 8) and Minitab (release 12) statistical packages and differences were considered significant with $\alpha \leq 0.05$.

RESULTS

Breeding density

Between 1996 and 1998, 22 Short-toed Eagle nesting territories were located in the study area. Table 1 summarizes the breeding densities of the eagles over the three years of the study. The mean nearest neighbour distance between nests was 3.4 km (range 0.75–7.12 km) in 1996, 3.06 km (range 0.75–6.56 km) in 1997 and 2.9 km (range 0.9–6.52 km) in 1998. These distances were not significantly different ($F_{2,46} = 0.44$, $P = 0.65$). For all years combined, the average nearest neighbour distance between nests was 2.7 km, and the range was 0.75–6.46 km. Thirty-eight per cent of the distances fell into the 1.5 to 2.5 km interval (Fig. 1). The shortest distance between two active nests was 750 m and the longest distance was 7120 m.

Regular dispersion of nesting territories was found in each study year in D-L-S forest complex ($G > 0.65$) (Table 1). For all 22 nesting territories the G-value was 0.757.

Breeding chronology

Eagles arrived in the nesting area between 18 March and 15 April (mean date = 31 March–1 April ± 6.5 days) (Table 2). The mean arrival date was significantly earlier in 1996 (24 March ± 3.9 days) than for the next

Table 1. Breeding density of Short-toed Eagles in Dadia–Lefkimi–Soufli forest complex in different years.

| | 1996 | 1997 | 1998 | All years |
|---|------------|------------|-----------|-----------|
| Pairs located | 17 (18) | 18 (21) | 17 (19) | 22 |
| Density (km ² /pair) | 20.6 | 17.7 | 19.6 | 16.9 |
| Mean nearest neighbour distance (km ± sd) | 3.4 ± 1.65 | 3.05 ± 1.8 | 2.9 ± 1.7 | 2.7 ± 1.5 |
| G statistic of regularity | 0.787 | 0.688 | 0.751 | 0.757 |

Numbers in parentheses were pairs monitored in the study area and include pairs for which the nest was not found or did not breed. These pairs are included in the density analysis, but not in the nearest neighbour distance and dispersion index analyses.

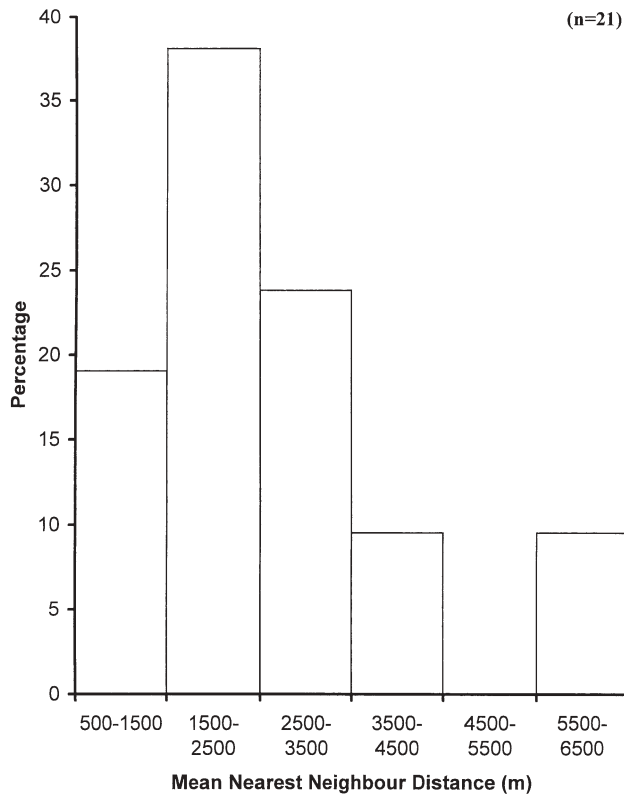


Figure 1. Percentage distribution of mean nearest neighbour nest distance for all years combined.

two years (1997: 4 April \pm 5.1 days; 1998: 4 April \pm 4.1 days) by about ten days (Fig. 2). The duration of the pre-laying period (mean \pm sd: 21.5 \pm 2.8 days) was similar in the three years. Breeding territories were established by eagles during the second week after their arrival and courtship and breeding activities began

during the last week before eggs were laid. The mean date of egg-laying was 21 April \pm 6.6 days. Mean laying-date was significantly earlier in 1996 (14 April \pm 4.7 days) than in 1997 (23 April \pm 5.5 days) and 1998 (25 April \pm 5.1 days) ($F_{2,49} = 17.85$, $P < 0.001$) (Fig. 2). The mean date of egg-laying (y) co-varied with the mean date of arrival (x) ($y = 0.9395x + 26.037$, $r = 0.904$, $P < 0.001$). The mean date of hatching was 6 June \pm 6.7 days, and was also significantly earlier in 1996 (30 May \pm 4.7 days) than in 1997 and 1998 (10 June) ($F_{2,36} = 23.35$, $P < 0.001$). The brooding period averaged 68.9 \pm 3.6 days ($F_{2,32} = 2.0$, $P = 0.15$); the shortest period was 63 days in 1997 and the longest period was 76 days in 1998. The mean fledging date was 12 August \pm 6.5 days. The first young left the nest on 28 July during 1996 and the last was fledged on 25 August during 1997. The mean fledging date was earlier in 1996 (6 August \pm 3.8 days) than in 1997 (15 August \pm 5.3 days) and 1998 (19 August \pm 3.4 days) ($F_{2,33} = 23.99$, $P < 0.001$). The median departure date was 19 September \pm 5.1 days. Median departure dates of Short-toed Eagles from the study area to the wintering places were similar in the three study years ($H = 4.16$, $df = 2$, $P = 0.12$). Earliest recorded departure date was 8 September 1997 and latest departure date was 2 October 1998. In 1996 an immature Short-toed Eagle remained in the nesting area until 8 October, whereas its parent left on 17 September.

The period between fledging dates and departure dates was about 39.6 days. As the result of earlier fledging dates in 1996, the period between fledging and departure was longer in 1996 (42.1 \pm 4.7 days) than in 1997 (38.2 \pm 4 days) and 1998 (36.9 \pm 3.1 days) ($H = 8.55$, $df = 2$, $P = 0.01$).

Table 2. Breeding chronology (mean day \pm sd and date) of Short-toed Eagles in Dadia–Lefkimi–Soufli forest complex during 1996–98.

| | 1996 | 1997 | 1998 | All years | Statistics ¹ |
|----------------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|----------------------------------|
| Arrival | 83.6 \pm 3.9 (24 March) | 93.8 \pm 5.1 (4 April) | 94.4 \pm 4.1 (4 April) | 90.9 \pm 6.5 (1 April) | $F_{2,58} = 35.69$, $P < 0.001$ |
| Laying | 104.9 \pm 4.7 (14 April) | 112.9 \pm 5.5 (23 April) | 114.6 \pm 5.1 (25 April) | 110.8 \pm 6.6 (21 April) | $F_{2,49} = 17.85$, $P < 0.001$ |
| Hatching | 150.6 \pm 4.7 (30 May) | 160.8 \pm 4.6 (10 June) | 160.7 \pm 4.2 (10 June) | 156.6 \pm 6.7 (6 June) | $F_{2,36} = 23.35$, $P < 0.001$ |
| Fledging | 219.1 \pm 3.8 (6 Aug.) | 227 \pm 5.3 (15 Aug.) | 231 \pm 3.4 (19 Aug.) | 224.4 \pm 6.5 (12 Aug.) | $F_{2,33} = 23.99$, $P < 0.001$ |
| Departure | 259.8 \pm 3.3 (16 Sept.) | 261 \pm 4.8 (18 Sept.) | 263.2 \pm 6.3 (20 Sept.) | 261.4 \pm 5.1 (18 Sept.) | $H = 4.16$, $P = 0.125$ |
| Pre-laying period | 22.4 \pm 1.5 | 21.2 \pm 3.2 | 21.1 \pm 3.4 | 21.5 \pm 2.8 | $H = 4.19$, $P = 0.124$ |
| Brooding period | 69.3 \pm 3 | 67.3 \pm 3.1 | 70.4 \pm 4.8 | 68.9 \pm 3.6 | $F_{2,32} = 2.0$, $P = 0.151$ |
| Post-fledging period | 42.1 \pm 4.7 | 38.2 \pm 4 | 36.9 \pm 3.1 | 39.6 \pm 4.7 | $H = 8.55$, $P = 0.014$ |

Day 1 = 1 January. ¹Data not meeting the assumptions of normality and homoscedasticity were analysed by Kruskal–Wallis test.

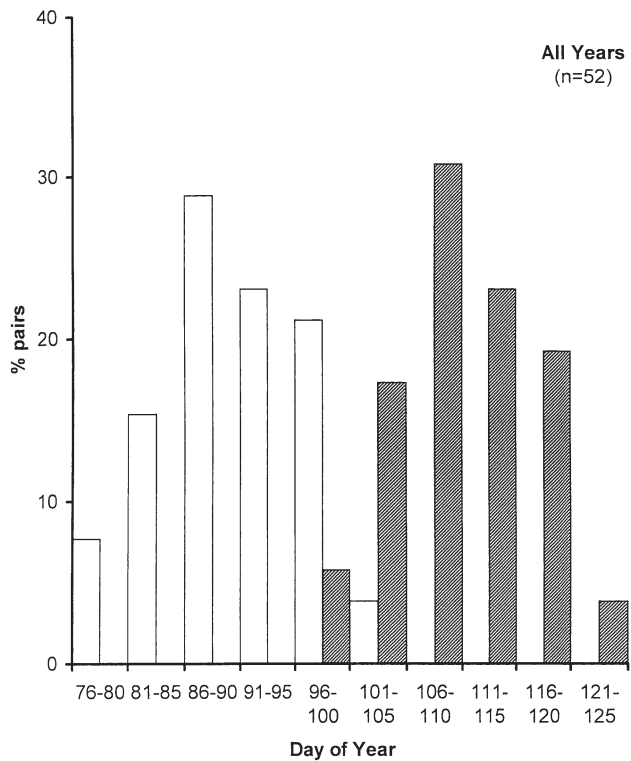


Figure 2. Arrival (□) and laying season (■) of Short-toed Eagles in Dadia–Lefkimi–Soufli forest complex during 1996–98. Arrival and laying dates were grouped into five-day periods with 1 January = day 1.

Overall breeding success

Of 58 Short-toed Eagle pairs monitored in the D-L-S forest complex, 52 pairs (90%) laid eggs in the three study years (1996–98) (Table 3). All clutches contained just a single egg ($n = 52$ nests). The mean productivity among years was 0.69 young per breeding pair. Sixteen pairs were unsuccessful, of which 81% of failures occurred at the egg stage and 19% occurred at nestling stage. No unsuccessful pairs produced a second clutch.

Breeding performance of Short-toed Eagles varied at different stages among years (Table 3). Seventy-five per cent of all eggs laid and 92% of all hatched eggs produced fledging eagles. The proportion of eggs hatched per egg laid (hatching success) was higher in 1996 than in 1997 and 1998 (2×3 contingency table; $G = 8.29$, $df = 2$, $P < 0.025$), although following a Bonferroni correction for multiple testing, this result becomes just non-significant. The proportion of young fledged per egg hatched (fledging success) was also higher in 1996 than in 1997 and 1998, but not significantly so (2×3 contingency table; $G = 3.37$, $df = 2$,

$P > 0.10$). The proportion of pairs successfully breeding was higher in 1996 than in 1997 and 1998 (2×3 contingency table; $G = 10.16$, $df = 2$, $P < 0.01$).

Thirteen clutches failed during incubation. In six clutches the single egg disappeared before hatching and in seven clutches the egg failed to hatch. Although most of the failures occurred in 1998 and 1997, the proportion of eggs that disappeared to eggs that failed to hatch was similar among years (2×3 contingency table; $G = 2.34$, $df = 2$, $P > 0.25$). There was no significant difference in the proportion of eggs failed (disappeared and added) to eggs successfully hatched between the clutches laid in the first and second halves of the breeding season (2×2 contingency table; $\chi^2 = 0.234$, $df = 1$, $P = 0.63$). In the eggs that failed to hatch, it was not possible to establish whether the eggs were infertile or whether the embryo died from overheating or overcooling. However, these eggs were incubated by the female for up to 64.4 days ($sd = 2.6$, $n = 7$). For all years combined, hatchability based on eggs remaining during incubation (excluding eggs that disappeared before hatch) was 84.8%, but it was higher in 1996 than in 1997 and 1998 (Table 3).

Most chick mortality occurred a few days after hatching. One young (one week old) fell from the nest when the nest split in two during a storm in 1997 and two disappeared from the nest. Although there was no direct evidence of predation, the two nests from which chicks disappeared were in the proximity of Eagle Owl *Bubo bubo* nests. There was no indication of nest robbing by humans as there were no marks on the trunks of the nest trees between consecutive visits to suggest that either tree had been scaled.

Productivity varied significantly among years. The average brood size at hatching and at fledging was higher in 1996 than in 1997 and 1998 ($F_{2,50} = 4.43$, $P = 0.02$ and $F_{2,49} = 5.07$, $P = 0.01$, respectively). The mean brood size at hatching was 0.75 young per pair and the mean brood size at fledging was 0.69 young per pair (Table 3).

Spring weather conditions during the study period

Climatic parameters in the study area varied widely from year to year (Table 4). Precipitation in April and May varied from 62.1 mm in 1996 to 225.6 mm in 1998 (208 mm falling in May). However, the fact that the number of rain days in 1998 was only marginally higher than in the preceding years indicates that a lot of this rain was torrential. In addition to (and possibly as a result of) the high rainfall the mean temperature in

Table 3. Breeding performance of Short-toed Eagles in Dadia–Lefkimi–Soufli forest complex during 1996–98.

| | 1996 | 1997 | 1998 | All years |
|--|-----------------|-----------------|-----------------|-----------------|
| No. territorial pairs ¹ | 18 | 21 | 19 | 58 |
| Pairs laying eggs (%) | 17 (94) | 18 (86) | 17 (90) | 52 (90) |
| Pairs hatching eggs (%) | 16 (94) | 14 (78) | 9 (53) | 39 (75) |
| Pairs fledging young (%) | 16 (100) | 12 (86) | 8 (89) | 36 (92) |
| Successful breeding pairs (%) | 16 (94) | 12 (86) | 8 (89) | 36 (69) |
| Unsuccessful breeding pairs (%) | 1 (6) | 6 (14) | 9 (11) | 16 (31) |
| Eggs disappeared before hatch (%) | 1 (6) | 1 (6) | 4 (24) | 6 (12) |
| Eggs added ² (%) | – | 3 (17) | 4 (24) | 7 (13) |
| Egg hatchability ³ (%) | 100 | 82.4 | 69.2 | 84.8 |
| Young disappeared or died (%) | – | 2 (14) | 1 (11) | 3 (8) |
| Nests failed at egg stage (%) | 1 (6) | 4 (2) | 8 (47) | 13 (25) |
| Nests failed at nestling stage (%) | – | 2 (11) | 1 (6) | 3 (6) |
| Mean (\pm se) brood size at hatching | 0.94 \pm 0.06 | 0.77 \pm 0.09 | 0.53 \pm 0.13 | 0.75 \pm 0.06 |
| Mean (\pm se) brood size at fledging ⁴ | 0.94 \pm 0.06 | 0.67 \pm 0.11 | 0.47 \pm 0.13 | 0.69 \pm 0.06 |

¹Total number of breeding pairs. ²Including infertile eggs or death of embryo by overheating or overcooling. ³Hatchability = [eggs hatched/(eggs laid – eggs disappeared before hatching)]. ⁴Productivity (mean young fledged per pair).

May 1998 was the lowest recorded in the study area for 35 years.

DISCUSSION

Population size and nest spacing

The population size of Short-toed Eagle is about 22 pairs in the D-L-S forest complex and the similar number of pairs that were recorded each year between 1996 and 1998 suggests that a stable population level is being maintained in the area. The population density in the study area (16.9 km²/pair) is one of the highest reported from Mediterranean countries. In southwest Spain, Amores & Franco (1981) estimated a density of 8.5 km² per pair, but their estimate was based on only six pairs. In contrast, Petretti (1988) found a much lower density of 48.6 km² per pair in central Italy ($n = 11$ pairs), and Cheylan (1981) found a density of 166.6 km² per pair in southern France. In fact, the

estimate of population density from the current study is similar to the estimate made by Vlachos & Papageorgiou (1994) (13.71 km² per pair, $n = 11$ pairs) for the Dadia forest reserve population. The mean nearest neighbour distance of the 22 breeding territories located in the D-L-S forest complex during the present study (MNND = 2.7 km) is much shorter than found in Belarus (MNND = 6 km, $n = 19$ pairs; Ivanovsky 1992), central Italy (MNND = 4.4 km, $n = 11$ pairs; Petretti 1988), and northwest Italy (MNND = 13–34 km, $n = 3$ pairs; Bocca 1989), but it was approximately the same as was found in the same area by Vlachos & Papageorgiou (1994) (MNND = 2.2 km, $n = 11$ pairs).

Short-toed Eagles are not strongly territorial and their home ranges overlap in the study area. Only a few nesting-site boundary disputes between pairs in close proximity were observed during this study, and individuals from different territories were frequently seen foraging over the same area. The nest dispersion pattern in the study area seems to be regular, confirmed by the G statistic ($G = 0.757$), even though a few pairs are in close proximity to each other. Many factors contribute to the nest spacing and the short nearest neighbour distances of Short-toed Eagles in the D-L-S forest complex. The undulating landscape with low hills and hundreds of gullies, and the extensive woodland cover with mature pine trees, seem to be important for suitable Short-toed Eagle nesting places, supporting a dense population in the area (Bakaloudis 2000). Food abundance and distribution are also well documented as influencing raptor dispersion (Newton 1979, 1991). In the study area, the abundance and

Table 4. Weather conditions in Dadia–Lefkimi–Soufli forest complex during the study period.

| | 1996 | 1997 | 1998 |
|-------------------------------|------|------|------|
| Mean temperature in May (°C) | 18.6 | 17.5 | 15.2 |
| Precipitation (mm) | | | |
| April | 61.3 | 73.7 | 17.6 |
| May | 0.8 | 21.6 | 208 |
| June | 0 | 19.1 | 38.6 |
| Number of rain days (>0.2 mm) | | | |
| April | 7 | 9 | 3 |
| May | 2 | 5 | 11 |
| June | 0 | 6 | 7 |

diversity of reptiles, which provide the bulk of food for Short-toed Eagles (Bakaloudis *et al.* 1998), are among the highest in Europe (Helmer & Scholte 1985). Moreover, regular nest dispersion has been observed in Sparrowhawks (Newton *et al.* 1977), Golden Eagles in Sweden (Tjebberg 1985) and northeast Scotland (Watson & Rothery 1986), and in Buzzards in north Wales (Dare & Barry 1990).

Breeding performance and success

The time of arrival of Short-toed Eagles in the study area (mid-March to mid-April) did not differ from that reported in literature (Choussy 1973, Cramp & Simmons 1980, Petretti 1988, Ivanovsky 1992, Vlachos & Papageorgiou 1994). The differences among years in the timing of arrival of Short-toed Eagles in the D-L-S forest complex during the present study may have been associated with the weather conditions in wintering quarters and on migratory routes (Elkins 1995). In addition, the activity of snakes and lizards after winter hibernation (mid-March) fits in with the timing of Short-toed Eagle arrival in the study area.

There are few published data on breeding success of Short-toed Eagle. However, the productivity of Short-toed Eagles in the D-L-S forest complex (0.69 young per pair) was lower than that found in previous studies. Petretti (1988) reported that Short-toed Eagles in central Italy produced an average of 0.75 young per pair, and Vlachos & Papageorgiou (1994) observed a productivity rate of 0.88 in northeast Greece. In the western Italian Alps Cattaneo (1998) found that the average number of young reared per reproductive pair was 0.74. The low overall reproductive output in the D-L-S forest complex during the study period was affected more by the low proportion of pairs that hatched eggs than the proportion of pairs that successfully fledged young. Furthermore, there was no improvement in the breeding success in pairs which laid eggs early in the season, as is found in Sparrowhawk (Newton & Marquiss 1984), Kestrel (Village 1986) and Peregrine Falcon (Mearns & Newton 1988).

In the present study, Short-toed Eagle breeding success was poorest when spring weather conditions were bad. Similar findings are documented for other raptors elsewhere. In Scotland, the proportion of Kestrel pairs that failed was positively correlated with total rainfall in May (Village 1986) and Sparrowhawk productivity was positively correlated with mean April temperature and number of rain-days in April (Newton

& Marquiss 1984, Newton 1989). In Germany, weather conditions also influenced the breeding success of Honey Buzzard (Kostrzewa 1989), Buzzard, Goshawk and Kestrel (Kostrzewa & Kostrzewa 1990). For Peregrine Falcon in Scotland, Mearns & Newton (1988) found that the overall breeding success varied according to rainfall in May, and in Australia Olsen & Olsen (1989) reported that July–September rain-days accounted for 60% of the variation in young fledged per territory, and the mean maximum temperature between August and October accounted for 74% of the variation in the percentage of territories from which young fledged. Steenhof *et al.* (1997), in southwestern Idaho, USA, found that the number of Golden Eagles fledged per pair was inversely related to the frequency of hot days (>32°C) in May and June.

Although there were only three years of breeding data, there is a suggestion from Tables 3 and 4 that cold, wet weather may influence Short-toed Eagle hatching success. This could occur directly by increasing the risk of chilling the embryo, particularly during changeovers. Low temperatures and rainfall can also affect Short-toed Eagle hatching success indirectly in two ways. First, the range of body temperatures of reptiles, especially snakes and lizards, is constrained by the range of environmental thermal conditions available (Brattstrom 1965, Zug 1993). As body temperature approaches critical thermal temperatures (minimum or maximum) an individual becomes sluggish and tends to become immobilized completely (Porter 1972, Zug 1993). Consequently, lower reptile activity as a result of low temperatures during the incubation period (especially May) would make them less vulnerable to Short-toed Eagles, which feed primarily on snakes and lizards. Although data for reptile density were collected on sunny and warm days, there was evidence that reptiles were less active during rainy days or low temperatures (Bakaloudis *et al.* 1998). Second, Short-toed Eagles themselves may have been encumbered by rain, because they were not observed to forage during rainy days during the three study years. Continuous or heavy rain may reduce hunting opportunities, decreasing either hunting efficiency or available foraging time (Newton 1979, Elkins 1995). Both of these factors lead to decreased prey delivery by the male to the incubating female. Extended periods of food shortage may prompt the female to abandon her nest or to increase the time far away from her egg to search for food. This would increase the probability of either chilling of the embryo or disappearance of the egg by predation (Eagle Owl, Raven *Corvus corax*).

However, Short-toed Eagle fledging success was not influenced by weather variables. The brooding period (mainly June and July) is associated with warm and dry weather and the peak of prey abundance (Bakaloudis *et al.* 1998), which increases the probability of eaglet survival and successful fledging. At this time (beginning of June to the middle of August) when food is plentiful, the young are protected much more efficiently by the female due to the decreased foraging time required. Particularly in some extreme cases of high temperature (>40°C), the female eagle stood over the young for the whole day.

The Short-toed Eagle breeding density in the D-L-S Forest in northeast Greece appears to be stable and one of the highest in Europe. Nevertheless, the combination of the small clutch size (only a single egg), the relatively low reproductive rate and a long period of immaturity (three to four years) could make the population susceptible to stochastic or human-induced factors. Consequently, it would be prudent to set up a long-term monitoring programme for the population.

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ENDNOTE

a. G-values range between 0 and 1, where values greater than 0.65 indicate regular nest spacing, while values less than 0.65 indicate a random distribution (Nilsson *et al.* 1982).

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