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Research Article

Breeding biology of Bonelli's Eagle (*Aquila fasciata*) in Cyprus

Savvas Iezekiel[1], Reuven Yosef[2,*], Dimitrios E. Bakaloudis[3], Malamati Papakosta[3,4], Christos G. Vlachos[3] and Andreas Antoniou[5]

[1]*Chief Conservator of Forests, Forestry Department of Cyprus Ministry of Agriculture, Rural Development and Environment, Louki Akrita 1414str., Cyprus*

[2]*Ben Gurion University of the Negev, Eilat Campus, P.O. Box 272, Eilat 88000, Israel*

[3]*School of Forestry and Natural Environment, Aristotle University of Thessaloniki, P.O. Box 241, 54124 Thessaloniki, Greece*

[4]*Wildlife Ecology & Management, Department of Forestry and Management of the Environment and Natural Resources, Democritus University of Thrace, Pantazidou 193, 68200 Orestiada, Greece*

[5]*Cyprus Association for the Protection of Avifauna, Kalamatas 10 Str., 8047 Paphos, Cyprus*

[*]*Corresponding author: ryosef60@gmail.com*

ORCID iDs: R. Yosef: 0000-0003-4331-9866; D.E. Bakaloudis: 0000-0002-0328-6871; M. Papakosta: 0000-0002-3223-6304

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Abstract The Bonelli's Eagle exhibits a wide geographic distribution yet remains relatively understudied on the island of Cyprus. Between 1999 and 2002, we examined 32 pairs of Bonelli's Eagles, totaling 64 breeding attempts. During this period, a total of 116 eggs were laid, with an average clutch size of 2.0 ± 0.1 eggs per pair. Incubation, predominantly performed by the female, lasted an average of 38.7 ± 0.2 days. Of the eggs laid, 71 hatched, resulting in an average hatching rate of 82.6%. Hatchability varied, with the highest rate (91.3%) observed in 1999 and the lowest (76.2%) in 2001. Nestlings spent an average of 61 ± 0.5 days in the nest before fledging. Remarkably, 92.6% of pairs successfully fledged young (n = 60), with a mean breeding success of 1.6 ± 0.1 fledglings per pair. Significant differences were observed in the average number of eggs laid, hatched, and young fledged between the two types of habitats. Nest sites varied in altitude, ranging from 170 to 1,242 meters, with a nearest-neighbor distance between adjacent nests averaging 7.86 ± 0.43 kilometers.

Keywords Bonelli's Eagle; *Aquila fasciata*; Cyprus; breeding

Introduction

The Bonelli's Eagle boasts a broad geographic distribution spanning from the Mediterranean to the Indo-Malayan regions. Despite extensive study in the western parts of its range, such as Spain (Real and Mañosa, 1997; Gil-Sánchez *et al.,* 2004; Palma *et al.,* 2006; López-López *et al.,* 2007; Martínez-Miranzo *et al.,* 2016; Morollón *et al.,* 2022), its status across its global range remains unclear (BirdLife International, 2019). Remarkably, the breeding population of Cyprus has been overlooked in many studies (e.g. Ferguson-Lees and Christie, 2001; Flint, 2019).

The Bonelli's Eagle stands as the sole large-sized eagle species known to breed on the island of Cyprus. According to Iezekiel *et al.* (2003), these eagles typically inhabit mountainous terrain, with nests often found at the forest edge, while hunting primarily occurs in more open areas. During dispersal, immature eagles tend to hunt in lowland garigue and agricultural areas, where prey is more abundant and accessible. In the context of Cyprus, the primary prey consists of birds and small rodents, as reported by Iezekiel *et al.* (2004).

Flint and Stewart (1992) also noted that during the late 1950s, the Bonelli's Eagle was considered common in Cyprus, with a population estimate of over 50 pairs, albeit based on anecdotal observations. However, a significant decline occurred in the 1980s to early 1990s, reducing the population to less than 20 pairs. Consequently, we initiated a study in the Pafos forest to explore the ecological requirements and constraints of Bonelli's Eagle on the island of Cyprus. Our objective was to investigate the breeding biology of this species in Cyprus, as we deemed it crucial to acquire such knowledge to propose effective management measures and feasible conservation plans for the protection of the Bonelli's Eagle population on the island.

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Figure 1. Spatial distribution of the breeding population of Bonelli's Eagle (*Aquila fasciata*) in Cyprus.

Methods

Our study is confined to the areas of the Republic of Cyprus under the effective control of the Government of the Republic of Cyprus. All breeding pairs of the Bonelli's Eagle were identified based on prior knowledge of the Pafos Forest (Figure 1), a substantial state-owned area spanning 62,000 hectares, primarily by Savvas Iezekiel (SI), who served as the Fauna Officer for the Department of Forests of the Cypriot Ministry of Agriculture, Rural Development, and Environment. The Pafos Forest is renowned for its high Bonelli's Eagle density, estimated at 2-2.5 breeding pairs per 100 km^2 (Iezekiel, 2003, 2011).

We classified a territory as occupied if we observed both adults near a nest, witnessed undulating courtship flights, or noted the delivery of nest material, as outlined by Fuller and Mosher (1987), during the years 1999-2002. Given sexual dimorphism, we presumed the larger individual of a pair to be the female, following the approach by Newton (1979). To minimize disturbance at the nest during the egg-laying and incubation periods, all nests included in the study were observed from distances of 50-100 meters. We meticulously monitored all breeding pairs throughout the entire reproductive cycle, from courtship to nest-building to fledging of young. Unhatched eggs were subsequently removed and examined for fertility using candling, as described by Ernst *et al.* (2004).

We defined a breeding attempt as the laying of at least one egg in the nest. Hatching success, or rate, was calculated as the percentage of all eggs laid that successfully hatched. Fledging success represented the percentage of all young hatched that successfully fledged (Newton, 1979; Steenhof and Kochert, 1982; Steenhof, 1987). Breeding success was determined by dividing the number of pairs that were successful by the total number of pairs that lay at least one egg.

Nest-building behavior was observed, and the substrate type (cliff face or tree) was noted. Egg laying and incubation behaviors were closely monitored using a telescope (X60) from vantage points positioned 50-100 meters away, allowing a clear view into the nest. During the incubation period, active nests were checked once a week, increasing to every 2-3 days in the final days before expected hatching. The exact hatching date was determined, considering the median date if a clutch hatched between visits. Observations continued in fledging territories, with the presence or absence of young checked every three days for the subsequent six months. The coordinates of the nests were recorded using a GPS device (Cramp and Simmons, 1980).

We computed the nearest-neighbor distance (NND) between breeding pairs for the years 2000-2002. To assess the statistical significance of these distances, we employed a G-goodness of fit test.

The mean nearest neighbor distance of adjacent pairs (MNDD) for each year of the study was compared using one-way ANOVA. Prior to each statistical test, the distances between nests were log-transformed [log (X + 1)] to ensure variance homogeneity. Additionally, the G statistic, derived from the ratio of the geometric mean to the arithmetic average of squares of distances between neighboring nests (Brown, 1975), was employed to assess the spatial distribution of Bonelli's eagle pairs in Cyprus.

All breeding variables were assessed for normality using the Anderson-Darling criterion and the Levene criterion for variance homogeneity. Variables were transformed as necessary to meet normality, utilizing the log transformation [log (X + 1)]. Differences in reproductive variables between groups were analyzed using either a one-dimensional analysis of variance (for normally distributed variables) or the Kruskal-Wallis non-parametric equivalent. Post-hoc tests, such as Tukey or Duncan's multiple range tests were employed to control for differences within each variable. Reproductive parameters expressed as frequencies or hatching rates were analyzed using contingency tables (chi-square test) to investigate variations among years of the study.

Mean ± standard error (SE) is presented throughout the text. Statistical analysis was performed using SPSS statistical software (release 19.0), with all tests being two-tailed and a significance level of $\alpha = 0.05$. For spatial analysis, we utilized ArcGIS.

Results

During the study period from 1999 to 2002, a total of 32 pairs of Bonelli's Eagles were studied. However, not all pairs were present or attempted to breed each year, resulting in varying annual sample sizes. Across the four years, a total of 95 occupied territories were documented (with 18, 25, 30, and 32 territories observed in 1999, 2000, 2001, and 2002, respectively). Breeding attempts were made in 64 of these territories, accounting for 67.4% of the total. Notably, 12 pairs (37.5%) nested during all four years of the study. Each nest was observed for an average of 46 ± 4.8 visits during each breeding season over the four years.

Reproductive success

During the study period, Bonelli's eagles exhibited courtship behavior, territory defense, and nest-building activities beginning in early November. The mean laying date for the study period was 9 February, with a deviation of ±2.6 days. Eggs typically hatched around 16 March, with a mean deviation of ±2.9 days, while fledging occurred around 18 May, with a similar mean deviation of ±2.9 days (Table 1). Following egg hatching, females continued to line the nest with twigs until the young fledged.

Table 1. Breeding success of 32 breeding pairs of Bonelli's Eagle (*Aquila fasciata*) in Cyprus, (1999-2002).[1]

Parameter		1999	2000	2001	2002	Average	Statistic	*P*-value
Egg laying date	Avg ± SD	32.0 ± 6.6	34.8 ± 5.0	47.4 ± 4.8	42.0 ± 4.4	40.1 ± 2.6	F3. 47 = 1.81	0.159
	Date	01-Feb	04-Feb	16-Feb	11-Feb	09-Feb		
	min-max			15-85	18-79	15-85		
	%CV	62.3	49.9	39.1	40.9	46.2		
	n	9	12	15	15	51		
Hatching date	Avg ± SD	71.3 ± 6.5	74.3 ± 6.7	74.1 ± 4.8	84.7 ± 5.3	76.4 ± 2.9	F3. 32 = 1.06	0.379
	Date	12-Mar	14-Mar	15-Mar	25-Mar	16-Mar		
	min-max	50-102	46-103	54-96	62-117	46-117		
	%CV	27.3	27	18.2	19.7	23.2		
	n	9	9	8	10	36		
Fledgling date	Avg ± SD	133.7 ± 5.6	138.9 ± 7.3	134.1 ± 5.6	144.9 ± 5.4	138.3 ± 2.9	F3. 30 = 0.86	0.472
	Date	14-May	18-May	14-May	24-May	18-May		
	min-max	115-161	110-167	110-154	123-177	110-177		
	%CV	12.5	13.9	10	11.8	12.3		
	n	9	7	7	10	33		
Hatching period	Avg ± SD	39.3 ± 0.4	38.7 ± 0.4	38.3 ± 0.5	38.5 ± 0.4	38.7 ± 0.2	F3. 32 = 1.31	0.289
	min-max	38-41	37-40	37-40	37-41	37-41		
	%CV	2.8	2.9	3.4	3.3	3.1		
	n	9	9	8	10	36		
Nestling period[2]	Avg ± SD	62.3 ± 1.1	63.4 ± 0.6	58.9 ± 0.8	60.2 ± 0.8	61.2 ± 0.5	F3. 29 = 5.14	**0.006**
	min-max	58-68	61-65	56-61	56-64	56-68		
	%CV	5.2	2.4	3.7	3.9	4.8		
	n	9	7	7	10	33		

[1] One-way ANOVA; SD = standard deviation; CV = coefficient of variation, n = sample size. Averages are presented in Julian dates.

[2] Bold value denotes significance greater than $P > 0.01$.

The mean clutch size, hatching rate, and brood size remained constant throughout the four years of the study ($P > 0.05$, Table 2). Across the 64 breeding attempts, a total of 116 eggs were laid, with an average clutch size of 2.0 ± 0.1 eggs per pair, ranging from 1 to 3 eggs per clutch.

Egg incubation lasted for approximately 38.7 ± 0.2 days (range 37-41 days, n = 36 pairs) and was predominantly conducted by the female, while the male was responsible for delivering food to the nest. Interestingly, in four instances involving three different pairs, females continued to incubate unfertilized eggs for extended periods ranging from 66 to 79 days. Out of the total 116 eggs laid, 71 hatched, resulting in an average of 1.7 ± 0.1 eggs per pair hatching successfully. The nestling period for Bonelli's Eagles in Cyprus was approximately 61 ± 0.5 days (ranging from 56 to 68 days, n = 33 nests).

Two pairs attempted a second breeding within the same season in separate instances. Specifically, in 2000, one pair abandoned their initial nest containing one egg, then after 46 days, laid two eggs in a nearby nest, which was also later abandoned. Similarly, another pair in the same year, after losing two hatchlings, laid one egg in a new nest after 64 days, which was subsequently abandoned. These addi-

Table 2. Breeding parameters of Bonelli's Eagle (*Aquila fasciata*) in Cyprus, 1999-2002.

Variable	1999	2000	2001	2002	Total
No. of territories	11	15	17	21	64
No. Pairs maintain nest	11 (100.0)	15 (100.0)	16 (94.1)	19 (90.5)	61 (95.3)
No. pairs laid eggs (%)	11 (100.0)	13 (86.7)	16 (100.0)	17 (89.5)	57 (93.4)
No. pairs hatch at least 1 egg (%)	10 (90.9)	10 (76.9)	9 (56.3)	12 (70.6)	41 (71.9)
No. pairs brood chicks successfully (%)	10 (100.0)	8 (80.0)	8 (88.9)	12 (100.0)	38 (92.6)
No. pairs reproduce successfully (%)	10 (90.9)	8 (61.5)	8 (50.0)	12 (70.6)	38 (66.7)
No. eggs laid	24	28	32	32	116
No. eggs not hatched (%)	1 (4.2)	10 (35.7)	11 (34.4)	8 (25.0)	30 (25.8)
No. infertile eggs (%)	2 (8.3)	4 (14.3)	5 (15.6)	4 (12.5)	15 (12.9)
No. eggs hatched (%)	21 (91.3)	14 (77.8)	16 (76.2)	20 (83.3)	71 (82.6)
No. chicks died (%)	4 (19.0)	3 (21.4)	3 (18.8)	1 (5.0)	11 (15.5)
No. chicks fledge (%)	17 (81.0)	11 (78.6)	13 (81.2)	19 (95.0)	60 (84.5)
No. pairs fledge 0 chicks	0	2	1	0	3
No. pairs fledge 1 chick	3	5	4	5	17
No. pairs fledge 2 chicks	7	3	3	7	20
No. pairs fledge 3 chicks	0	0	1	0	1
Mean clutch size (± SD)	2.2 ± 0.1	2.2 ± 0.2	2.0 ± 0.1	1.9 ± 0.1	2.0 ± 0.1
Mean clutch size at hatching (± SD)	2.1 ± 0.2	1.4 ± 0.2	1.8 ± 0.2	1.7 ± 0.1	1.7 ± 0.1
Mean young fledge (± SD)	1.7 ± 0.2	1.4 ± 0.2	1.6 ± 0.3	1.6 ± 0.2	1.6 ± 0.1
Mean breeding success (± SD)	1.6 ± 0.2	0.9 ± 0.2	0.8 ± 0.3	1.1 ± 0.2	1.1 ± 0.1

tional breeding attempts by the two pairs were excluded from the analyses conducted in the study.

A relatively high percentage, precisely 92.6% (n = 60) of pairs that hatched at least one egg successfully fledged young. The mean number of fledglings per pair was 1.6 ± 0.1.

We observed a relatively high level of territory and nest-site reuse in our study. Specifically, 41% of the Bonelli's Eagles nested at the same site in all four breeding seasons, while 18% did so during three out of the four study years.

The mean nearest neighbor distance between neighboring nests was 9.31 ± 0.64 km in 2000, 8.2 ± 0.5 km in 2001, and 7.87 ± 0.43 km in 2002 (Table 3). The shortest distance between two neighboring pairs was 3.93 km, while the farthest was 13.47 km. However, the differences between years were not statistically significant (T-test t = 1.056, DF = 2, $P = 0.402$).

After each breeding season, a total of 13 unhatched eggs were collected from the nests, with varying numbers recorded across the years: 2 in 1999, 6 in 2000, 5 in 2001, and 2 in 2002. Upon examination using candling, it was determined that the majority of these eggs, 11 (84.6%), were infertile. Additionally, one egg exhibited a deceased embryo (7.7%), while another egg was found to lack a calcareous shell (7.7%).

Discussion

Our study on the reproductive success of the Bonelli's eagle in Cyprus provides valuable insights into the factors influencing their breeding outcomes. The relatively high reproductive success rate observed in our study (1.1 ± 0.1 young/breeding pair) aligns with findings from other regions where the species is studied – Spain (Parellada *et al.,* 1996; Real and Mañosa, 1997, Penteriani *et al.,* 2003; Gil-Sánchez *et al.,* 2004; López-López *et al.,* 2006), France (Real *et al.,* 1996), Morocco (Bergier and Naurois, 1985), and Israel (Leshem, 1976).

Factors such as the rate of failure during egg incubation (18%) and brooding (7%) stages contribute to overall reproductive success. Similar low chick mortality rates have been reported in other raptor species (*Aquila pomarine* – Vlachos, 1989; *Circaetus gallicus* – Bakaloudis *et al.,* 1998; Bakaloudis, 2000) and are influenced by various intrinsic and extrinsic factors (human disturbance, inclement weather, lack of prey, etc.), including energy investment by the birds, human disturbance, inclement weather, and prey availability (Newton, 1979, 1998; Steenhof *et al.,* 1997; Carrete *et al.*, 2002a).

Of the 13 unhatched eggs retrieved from the nests, most were determined to be infertile. Among them, one contained a deceased embryo, and another was discovered to lack a calcareous shell. These findings offer insight into the breeding success of Bonelli's Eagle population in Cyprus, indicating the common occurrence of infertility and sporadic embryonic abnormalities, which could impact reproductive outcomes.

The correlation between reproductive success and prey availability, distribution, and accessibility underscores the importance of prey species in determining breeding outcomes for eagles. Areas with abundant prey species, such as agricultural and low-altitude habitats (e.g. scrublands, grasslands), may experience earlier onset of breeding compared to forested areas at higher altitudes, as prey availability influences the timing of breeding activities (Newton, 1979; Dijkstra *et al*., 1982; Korpimäki, 1987; Steenhof *et al.*, 1997). Understanding these ecological dynamics is crucial for effective conservation and management strategies for Bonelli's eagles and other raptor species.

The increasing trend in the number of breeding territories observed in our study suggests a potential recovery of Bonelli's Eagle population in Cyprus. This positive trend is particularly significant considering the historical decline reported in the late 20th century, where the population dwindled to fewer than 20 pairs due to various anthropogenic pressures such as development, habitat degradation, and disturbance. The observed increase in breeding territories indicates a positive response to conservation efforts and habitat management strategies implemented in recent years. It also highlights the resilience of the Bonelli's Eagle population in the face of past challenges. Continued monitoring and conservation measures will be crucial to ensure the continued recovery and stability of the population. The historical context provided by Flint and Stewart (1992) underscores the importance of long-term monitoring and conservation efforts in mitigating threats to wildlife populations. By addressing underlying factors contributing to population decline, such as habitat loss and disturbance, ongoing conservation initiatives can help sustain and enhance the recovery of Bonelli's Eagle population in Cyprus (Kassinis, 2010).

The findings from both Kassinis (2010) and our study underscore the importance of sizeable Calabrian pine trees (> 15 m high) as preferred nesting sites for Bonelli's Eagles in Cyprus. The majority of breeding pairs in both studies chose these trees as their nesting substrate, highlighting the significance of this habitat feature for the species. The relatively low proportion of breeding pairs

Table 3. Nearest-neighbor-distance (m) amongst nest-sites of Bonelli's Eagle (*Aquila fasciata*) in Cyprus.

Parameter	2000	2001	2002	Overall
n	25	30	32	32
mean distance (m)	9,306.44	8,281.10	7,871.63	7,863.53
Range	4,233-16,790	3,926-13,600	3,926-13,400	3,926-13,470
SD	3,199.10	2,659.52	2,478.33	2,427.08
G-statistic	**0.885**	**0.901**	**0.908**	**0.911**

nesting on cliffs (18%), as observed in both studies, suggests that while cliffs may serve as suitable nesting sites for some individuals, they are less preferred compared to large pine trees. The remote and extensive nature of cliff formations described by Kassinis (2010) aligns with the nesting habitat preferences observed in our study. Understanding the habitat preferences and nesting behavior of Bonelli's Eagles is essential for effective conservation planning and habitat management. By identifying and protecting key nesting sites, such as large pine trees and remote cliff formations, conservation efforts can focus on preserving critical habitat features essential for the breeding success and population viability of the species.

The observed high territory and nest-site re-use in our study is indeed noteworthy, highlighting the species' ability to persist and adapt in its habitat. However, the evidence of anthropogenic disturbance leading to nest or territory desertion underscores the significant impact of human activities on the breeding success and population dynamics of Bonelli's Eagles. Incidents such as nests being destroyed, eggs removed, and breeding adults subjected to poisoning or shooting pose severe threats to the species' conservation (S. Iezekiel, unpublished data; Kassinis, 2010). The findings by Perona *et al.* (2019) suggesting increased home range and time away from nests during weekends and holidays in Bonelli's Eagles in Spain indicate potential behavioral responses to human disturbance. However, this contrasts with the conclusions drawn by Carrete *et al.* (2002b) and Muñoz and Real (2013), who did not find a significant influence of human presence on the distribution of Bonelli's Eagle populations. These discrepancies may reflect variations in study methodologies, environmental contexts, and local human-wildlife interactions across different study sites. Overall, the coexistence of Bonelli's Eagles with human activities highlights the need for effective conservation measures to mitigate anthropogenic threats and ensure the long-term survival of the species. Habitat protection, enforcement of regulations against wildlife persecution, and raising awareness among local communities about the importance of conserving these iconic raptors are crucial steps in safeguarding Bonelli's Eagle populations.

The lack of significant effects of elevation on egg laying ($r^2 = 0.085$), hatching ($r^2 = 0.004$), and fledging success ($r^2 = 0.0005$) in our study area suggests that the warm and dry Mediterranean climate may have homogenized the breeding parameters across different elevations for Bonelli's Eagles. This contrasts with findings from Spain, where altitude and distance from the sea were associated with differences in clutch initiation dates and productivity. In Spain, pairs nesting at lower elevations or near the sea initiated egg-laying earlier and exhibited greater productivity compared to those at higher altitudes and inland locations (Ontiveros and Pleguezuelos, 2003a,b). Similarly, López-López *et al.* (2007) reported higher breeding success for pairs at lower altitudes. These discrepancies highlight the importance of considering regional climatic variations and ecological factors when studying the breeding ecology of raptor species like Bonelli's Eagles. Local environmental conditions, including temperature, precipitation, and habitat characteristics, can significantly influence breeding behaviors and reproductive outcomes. Further research incorporating such factors is essential for a comprehensive understanding of the species' ecology and conservation needs across different geographical regions.

The average nearest neighbor distance of 7.9 km observed in our Bonelli's eagle population on Cyprus is shorter than that reported for other regions, such as Murcia in south-eastern Spain (15.6 km, Carrete *et al.,* 2002b) and Castellón province (7.7 km, López-López *et al*., 2004). This suggests that the eagle population on the island may be close to carrying capacity (see Hernández-Matías *et al.,* 2013). Carrete *et al.* (2002b) and Lopez-Lopez *et al.* (2004) proposed that their populations in Spain were sparsely distributed, primarily due to inter-specific competition with sedentary populations of Golden Eagle (*Aquila chrysaetos*). The shorter nearest-neighbor distance observed in our study may indicate a higher density of Bonelli's eagle pairs in the study area compared to these regions, possibly due to differences in habitat suitability, prey availability, or other ecological factors unique to Cyprus. Further investigation into the underlying mechanisms driving population density and distribution patterns would provide valuable insights into the ecology and conservation of Bonelli's eagles on the island.

In conclusion, Bonelli's eagle population in Cyprus exhibits signs of stability and viability based on the findings of our study. However, further research is warranted to gain a comprehensive understanding of the species' current status on the island. Specifically, additional studies should focus on assessing the dispersal patterns of young eagles and investigating the potential establishment of breeding populations in the central and eastern parts of Cyprus. By addressing these knowledge gaps, conservation efforts can be better informed to ensure the long-term persistence and well-being of Bonelli's eagle population on the island.

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