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Selection of breeding cliffs by Griffon Vultures *Gyps fulvus* in Crete (Greece)

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Abstract. A multivariate analysis was carried out in order to investigate the most influential habitat variables and related features in the selection of breeding cliffs by the Griffon Vulture in Crete. The species was found nesting in mid-altitude areas, close to stock-raising units, on high limestone cliffs, which were also well protected against the prevailing winds of the island. A principal components analysis, which explained 53% of the total variance of the variables examined, differentiated Griffon Vulture colonies in relation to their isolation from other colonies, accessibility to humans and proximity to food resources. In addition, a stepwise discriminant function analysis between breeding and random cliffs included the height of the cliff, its substratum, the altitude, and the distance to the stock breeding unit in a model that successfully classified 97.1% of the nesting and 88.2% of the random cliffs. In comparison to continental regions the Griffon Vulture colonies in Crete were located on higher cliffs but at a lower altitude. This fact should be attributed to the species nesting on steep coastal cliffs close to the livestock's wintering areas.

Key words: Griffon Vulture, *Gyps fulvus*, nest sites, breeding, Crete

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INTRODUCTION

The Griffon Vulture is a colonial cliff-nesting raptor that inhabits Eurasia and north Africa (Cramp & Simmons 1980, Mundy et al. 1992). It feeds primarily on carcasses of medium and large-sized animals (Donázar 1993). Its European population is estimated at about 21,000 breeding pairs, which are mainly distributed along the Mediterranean basin, with the Iberian peninsula being the species' stronghold (BirdLife International 2004). In Greece, the Griffon Vulture population numbers no more than 300 pairs (Handrinos & Akriotis 1997) after having suffered a sharp decline in the 1960s and 70s, due to secondary poisoning during anti-predator campaigns (Handrinos 1985). At present, according to the Greek Red Data Book, the species is considered as endangered (Handrinos 1992) with the island of Crete harboring the most significant subpopulation in the country (i.e. 141 breeding pairs, Xirouchakis & Mylonas 2005). This fact has been attributed to the low use of poisoned baits for vermin and the existence of suitable foraging and nesting habitat. However land use changes have been dramatic on the island, especially after 1981 when Greece joined the European Union, which resulted in a reduction and degradation of rangelands (Ispikoudis et al. 1993, Lyrintzis 1996). Land use changes can reduce the carrying capacity of the habitat although food availability is not always the deterministic factor in population growth (Newton 1991). In the case of cliff nesting species nest site suitability may be more influential in determining their distribution and density (Newton 1979). Nesting habitat descriptions for Griffon Vulture are generally scarce (Donázar 1987, Donázar et al. 1989), while in Greece, relevant accounts are lacking. Griffon Vultures' nesting and roosting habitat has been described for the island of Crete (Xirouchakis & Mylonas 2004), though the most influential factors that determine their selection have not been investigated.

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The aims of the present study have been to determine preferential requirements in macro- and microhabitat scale in the use of nesting cliffs by the Griffon Vulture in Crete, to elucidate any differences in site selection compared to continental populations, to assess any structure in the distribution of colonies and to provide preliminary data for constructing predictive distribution models in the future.

STUDY AREA

The study area comprised the island of Crete (8261 km^2), located in the south Aegean (34°54′ and 35°41′N, 23°30′ and 26°19′E). The rugged terrain geomorphologically characterizes the island with three major massifs spreading from east to west: Lefka Ori (2452 m a.s.l.), Psiloritis (2456 m a.s.l.) and Dikti (2148 m a.s.l.). The climate is typical Mediterranean with mild winters and hot and dry summers. The mean annual temperature varies between 8° C and 20° C. However, the mean annual difference between the coastal areas to the inner mountain regions decreases by a rate of 6° C per 1000 m a.s.l., whereas the respective difference between the north and south parts is 2° C (Pennas 1977). The vegetation is dominated by garrigues (e.g. *Sarcopoterium spinosum*, *Cistus* spp., *Euphorbia* spp., *Plhomis fruticosa*, *Satureja thymbra*) and to a lesser extent by dry-leafed maquis (e.g. *Quercus coccifera*, *Pistacia lentiscus*, *Ceratonia siliqua*, *Erica arborea*, *Juniperus* spp.). The most common tree species are the wild Olive *Olea europea* var. *sylvestris*, the Carob tree *Ceratonia siliqua*, the Calabrian Pine *Pinus brutia* and the Kermes Oak *Quercus coccifera*. However olive groves, which have locally expanded up to 800 m in conjunction with fire and overgrazing, have caused the shrinkage of the boundaries between garrigues and maquis and have resulted in the overdominance of low spiny shrubs such as the Thorny Burnet *Sarcopoterium spinosum* and the Cistus *Cistus creticus* and *Cistus salvifolius* which are resistant to grazing and adapted to fire (Egli 1997, Tsiourlis et al. 1997).

MATERIALS AND METHODS

Overall, 34 cliffs were surveyed in 2003 where breeding activity of vultures was recorded at least once between the years 1996 and 2002 (Fig. 1). The cliffs were located with a GPS, plotted on 1:50 000 topographic maps (Geographic Service of the Hellenic Army) and a geological map of Crete (Bonneau 1976) and were described with reference to some habitat variables (Table 1) that were obtained through a Geographic Information System (Arc/View 3.2, ESRI 1996). Additional data on a microhabitat scale (absent from the maps) were collected in the field. The precipitation was

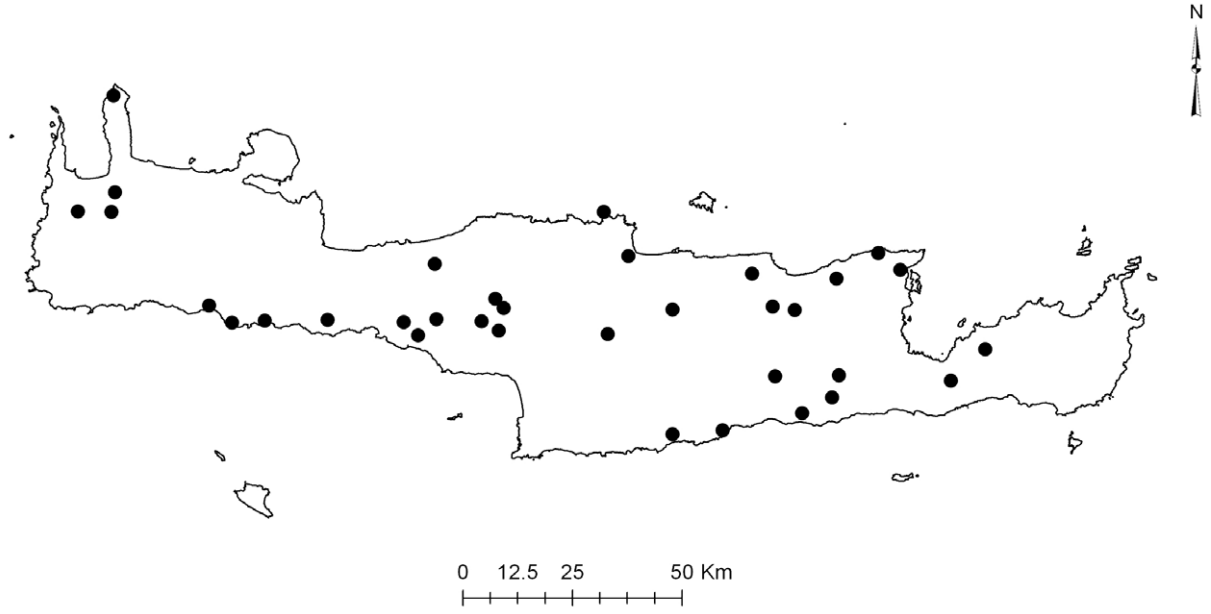


Fig. 1. Distribution map of the Griffon Vulture colonies in Crete (2003).

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Table 1. Descriptive parameters and habitat variables examined at the Griffon Vultures' colonies (i.e. nesting cliffs) in Crete.

Variable	Description
Substratum	Pedrock of the cliffs used by the griffons (1 = Dolomitic limestone, 2 = Calcareous pebble conglomerates, 3 = Platy limestone/marble)
Height	Distance between cliff peak and base (m) measured by the use of clinometer
Altitude	Distance from sea level (m)
Exposure	Cliff orientation measured in compass azimuths
Relief	Topographic heterogeneity index (i.e. the total number of 20 m contour lines intersected by four vertical 1-km routes, starting from the main roost towards the four directions)
Wind	Classification according to the protection form the prevailing winds of Crete (0 = N or NW, 1 = NE or W, 2 = E, 3 = SW, 4 = S or SE)
Sea	Distance of the cliff base from the coast (km)
Asphalt	Distance from the nearest paved road (km)
Road	Distance from the nearest road (km)
Pastoralism	Distance from the nearest stock-raising unit (km)
Settlements	Distance from the nearest human settlement (km)
Population	Number of inhabitants of the nearest settlement
Nearest colony	Mean nearest distance to neighbour colony (km)

not included in the analysis as local conditions in nesting cliffs differed greatly from the available meterological data acquired for the respective areas. In addition, the distance of nesting cliffs to stock breeding units was used to assess the effect of food on the species, as griffons feed on livestock carcasses, which are thrown in local dumps from nearby stocking farms (pers. obs.). Livestock numbers around the colonies' area was not used as an index of food abundance since the foraging ranges between neighbouring colonies overlapped.

An equal number of cliffs were selected at random by generating random X–Y coordinates in a computer (Snedecor & Cochran 1967). In case a random site was located on flat ground, the nearest cliff was selected. Each site was placed ca. 11 km from any known colony (i.e. the mean minimum nearest neighbour distance) or previously selected random cliff in an effort to minimize spatial autocorrelation. Variables with negatively skewed distributions were square root transformed whereas those with positive ones were log transformed i.e. [log (x+1)] (Daniel & Wood 1980). All variables were examined for normality by using Kolmogorov-Smirnov tests. A univariate analysis was carried out where the mean values of the data for nesting and random cliffs were compared using t-tests and the Watson-William's multiscaling testing of angles for their aspect (Zar 1996).

A stepwise discriminant function analysis was used with a forward variable selection and a tolerance value of 0.05 in order to obtain the best subset of habitat-related explanatory variables in separating nesting cliffs form random cliffs. In the dependent variable, the two types of cliffs were grouped using categorical data (i.e. nesting cliff = 1, random cliff = 0). The discriminant power of the explanatory variables was tested by the use of the Mahalanobis D^2 procedure (which also adjusts for unequal variances) and by ranking the partial *F*-values that indicate the associated level of significance for each variable. The equality of variance/covariance matrices of the data was examined by applying the Box's M test. Highly correlated variables (i.e. ≥ 0.60) were omitted in an attempt to treat multicollinearity. Finally a U-method was conducted (i.e. each case in the analysis is classified by the functions derived from all cases other than that case) in an effort to check the success of the classification procedure.

A principal component analysis was also performed to classify the nesting cliffs and investigate their distribution pattern by identifying which combinations of the habitat parameters could explain the largest amount of variation (Ludwig & Reynolds 1988, Fowler et al. 1998). Continuous variables were standardized ($Z_i = x_i\text{-}\bar{x}/SD$), so they could be treated as being equally influential, and were tested for multicollinearity and multivariate normality using the Bartlett's test of sphericity. A scree plot was used to identify break points separating the most important components from the rest. Principal components with eigenvalues > 1.0 were retained and rescaled with the varimax approach in order to obtain an orthogonal rotation of factors (Manly 1986). Variables loadings

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greater than 0.5 were considered to be of higher significance.

Nominal variables were tested by contingency tables, applying Yates's correction wherever the degree of freedom was one (Zar 1996). All statistical analyses were performed with SPSS 12.0 (Norussis 1989).

RESULTS

Univariate analysis indicated significant differences between nesting cliffs and random cliffs related to altitude, cliff height, relief, distance to the nearest stock-raising unit, and wind protection. Compared to the set of random cliffs, the griffons were found nesting at a lower altitude on dolomitic limestone cliffs (χ^2 = 21.6, df = 2, $p < 0.001$) of greater height and in more rugged terrain (Table 2). In addition, they were located closer to stock-raising units and were better protected against the north winds of Crete (Table 2). However, the mean orientation of nesting cliffs ($\bar{x}$ ± a.d.= 167.4° ± 54°) did not differ significantly from the mean orientation of random cliffs ($\bar{x}$ ± a.d.= 11.9° ± 68° , Watson $U^2 = 0.10$, $p > 0.05$).

The stepwise discriminant function analysis included the height of the breeding cliff, its substratum, the altitude and the distance to stock-breeding unit in a model that best explained the differences between the breeding and the random cliffs (Wilk's Lambda = 0.25, $p < 0.001$, R = 0.86, Table 3). The method classified successfully 97.1% of the colonies and 88.2% of the random cliffs. The overall correct classification was 92.6%.

The principal components analysis led to the retention of five components with eigenvalues higher than one, which explained 74% of the total variance of the variables that described nesting cliffs. However, the scree plot separated the first three from the rest, with eigenvalues > 1.5 and explaining 53% of the total variance (Table 4). Factor I absorbed 19% of the total variance with important variable loadings for the distance to asphalt roads, the distance to settlements and the distance to the nearest active colony. Factor I could be interpreted as a "competition-remoteness" variable and distinguished colonies in relation to their isolation. High or low values in Factor I indicated colonies away or close to human installation and other colonies. Factor II absorbed 17% of the total variance and was specified by the distance to the sea and the distance to the nearest stock-raising unit. Factor II could be characterized as "altitude-food" variable and differentiated the colonies according to their proximity to food resources. High and low values in Factor II indicated colonies located in mountainous regions or coastal cliffs and away or close to pastoral activity. Factor III contributed an additional 16% to the cumulative variance of the two leading factors and was determined by the height of the cliffs, the ruggedness of the terrain and the distance from the nearest road. Factor III could be interpreted as a "relief-accessibility" variable and

Table 3. Discriminant function analysis of the habitat characteristics of Griffon Vultures' breeding cliffs and random cliffs in Crete.

Variables	Min D^2	Discriminant function coefficients	F	p
Constant		-1.02		
Height	5.7	-3.51	97.4	< 0.001
Substratum	8.4	0.65	70.1	< 0.001
Altitude	10.3	2.06	56.9	< 0.001
Pastoralism	11.3	2.01	46.3	< 0.001

Table 2. Habitat characteristics of Griffon Vulture nesting cliffs (N = 34) and random cliffs (N = 34) in Crete. * — $p < 0.05$, ** — $p < 0.01$, *** — $p < 0.001$.

Variable	Nesting cliffs			Random cliffs			
	$\bar{x}$ ± SD	Min	Max	$\bar{x}$ ± SD	Min	Max	t-test
Altitude (m)	453 ± 225	120.0	1100.0	651 ± 464	140.0	1840.0	2.22*
Height (m)	170 ± 89	60.0	400.0	51 ± 30.8	20.0	140.0	7.36***
Relief	58 ± 10	41.0	83.0	46 ± 15	25.0	92.0	3.66***
Wind	2.91± 1.44	0.0	4.0	1.5 ± 1.5	0.0	4.0	3.86***
Sea (km)	5.8 ± 5.1	0.06	20.2	8 ± 5.4	0.68	21.0	1.72
Asphalt (km)	1.56 ± 2.00	0.10	12.2	6.1 ± 25.4	0.05	150.0	1.04
Road (km)	0.56 ± 0.74	0.08	4.3	6± 32.4	0.01	190.0	1.03
Pastoralism	1.5 ± 1.3	0.40	6.5	2 ± 1.18	0.8	5.6	2.66**
Settlements	1.77 ± 1.74	0.52	11.2	17 ± 86.6	0.16	507.0	1.00
Population	165 ± 157	10.0	642.0	251 ± 545	2.0	2507.0	0.85
Nearest colony (km)	10.3 ± 5.3	1.80	23.6	9.8 ± 5.0	4.7	31.5	0.48

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Table 4. Variables of Griffon Vulture breeding cliffs in Crete used in an analysis of principal components (with eigenvalues > 1.5) and varimax-rotated factor loadings with absolute values (underlined) used to interpret discrimination.

Variables	Principal components		
	I	II	III
Substratum	-0.196	-0.081	-0.019
Altitude	-0.262	0.706	0.246
Height	-0.118	-0.169	0.786
Exposure	0.069	-0.057	-0.001
Relief	-0.075	0.369	0.747
Wind	-0.453	-0.058	0.047
Sea	-0.202	0.823	-0.133
Asphalt	0.870	-0.194	0.201
Road	0.130	-0.161	0.830
Pastoralism	-0.057	-0.758	-0.076
Settlements	0.907	-0.051	-0.039
Population	0.027	0.488	-0.202
Nearest colony	0.696	0.000	-0.170
Eigenvalues	2.90	2.08	1.42
% Total variance	19.0	17.0	16.0
% Cumulative variance	19.0	36.0	53.0

divided the colonies according to the steepness of the cliff and its proximity to human activities. High and low values in Factor III indicated colonies located in upland uninhabited areas and those located in the urbanized lowlands.

DISCUSSION

The results of the present study show that the selection of nesting cliffs by the Griffon Vulture in Crete is not random. The location of the colonies is determined primarily by the cliffs' morphology and substratum. Cliff height is fundamental for a species of such size and weight (Cramp & Simmons 1980). High vertical cliffs generate strong updrafts and produce optimum flight conditions for soaring raptors (Pennycuick 1973, 1998). In comparison to other European populations, griffons in Crete select cliffs located at lower altitude but of greater height (Kostin 1983, Vitovich 1985, Arroyo et al. 1990, Seco & Vadillo 1990, Marinkovič & Orladič 1994, Tucker & Heath 1995). These differences should be attributed to the ruggedness of the terrain in low and middle altitude areas up to the coastline. The exposure of the nesting cliffs generally followed the orientation of the cliff wall or the axis of the gorge, though always avoided adverse weather conditions (i.e. north winds). This pattern is common among griffon colonies in continental Europe (Leconte 1977, Vitovich 1985, Marinkovič & Orladič 1994) apart from Spain where the population has reached its carrying capacity and rocks are occupied by the vultures regardless of their orientation (Donázar & Fernández 1990, Donázar 1993, Parra & Telleria 2004). The cliff's substratum proved also to be crucial for nest site selection. Cliffs of dolomite limestone were excessively used by griffons, probably due to the existence of various rock formations (e.g. potholes, ledges with overhang) that were suitable for nesting. This phenomenon is caused by the high susceptibility of limestone to water erosion (Xirouchakis & Mylonas 2004). In fact, almost all eroded limestone cliffs on the island (that bear the characteristic orange color of the exposed iron oxides of the underneath substratum) had signs of vulture use (e.g. whitewashes).

Overall, it seems that Griffon Vultures occupied the best cliffs in terms of flight conditions, wind protection and site quality as the substratum has been a significant factor in determining the breeding performance of colonial species (Rodenhouse et al. 1997, Fernádez et al. 1998, Newton 1998, Hanna et al. 2004). However, in contrast to cliff quality, discriminant factor analysis indicated that the proximity to food resources possessed the least discrimination ability (e.g. least partial *F*-value and least maximization of Mahalanobis distance between data groups), thus food availability should not be considered as a critical factor in cliff site selection. This result is consistent with regions of continental Europe where colonies are also restricted on calcareous sectors, which in some cases are more crucial in limiting the species' breeding range than food availability (Leconte 1985, Donázar et al. 1989, Donázar & Fernádez 1990, Parra & Telleria 2004). Griffons of the genus *Gyps* are able to forage great distances away from their nesting sites which can be confined on the most suitable cliffs in the broader area (Houston 1974, Robertson & Boshoff 1986, Donázar 1993, Bahat & Kaplan 1995). The explanatory variable of food availability probably reflected the overlap between areas of pastoral activity and the species' breeding habitat. More specifically, the wintering areas of the livestock spread from the coastline up to 600 m a.s.l., while many precipices and gorges (ca. 90) are located at the periphery of the mountains (< 600 m) or drive out to the sea. Furthermore the rocky terrain of the island that covers ca. 60% of its surface, comprises largely of limestone (i.e. 45–50%, Fasoulas et al. 1994, Fasoulas 2001), thus several high vertical cliffs are suitable for nesting. This is also depicted by the fact that 76% of the griffon colonies are distributed below the

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600 m contour, while 41% of them are located in gorges and 26% on steep offshore rocks (Xirouchakis 2003).

Similarly, in the principal component analysis, cliff height and the relief of the landscape showed up in the third factor (while the substratum in the fifth), which absorbed the smallest part of the total variance. These habitat features provided the least differentiation among breeding cliffs and should be regarded as prerequisite for their selection. However, the analysis revealed that griffon colonies could be divided into two broad categories in relation to their distribution: a) colonies located in the interior of the island in remote uninhabited areas and b) those that are located in agricultural areas of the lowlands close to the coastline and the urban zone. In both cases further classification could be made by food availability and intraspecific competition.

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STRESZCZENIE

[Wybór miejsc gniazdowych przez sępy płowe na Krecie]

Liczebność europejskiej populacji sępa płowego szacowana jest na około 21 tysięcy par lęgowych rozmieszczonych głównie w basenie Morza Śródziemnego. W Grecji liczebność tego drapieżnika nie przekracza 300 par. Jak dotąd jedynie nieliczne prace dotyczyły wybiórczości środowiskowej stanowisk lęgowych. Celem pracy było określenie preferencji w skali makro- i mikrohabitatowej, znalezienie różnic między populacją kreteńską a populacjami kontynentalnymi oraz prawidłowości w rozmieszczeniu kolonii lęgowych.

W 2003 skontrolowano 34 klify, gdzie w latach 1996–2002 znajdowano gniazda tych drapieżników. Dla wszystkich stanowisk opisano 13 cech: rodzaj skał, topografię, wysokość klifu, wysokość nad poziomem morza, ekspozycję, przeważający kierunek wiatrów, odległość do wybrzeża, najbliższej szosy, drogi, farmy hodowlanej, osiedli ludzkich, liczbę ludności w najbliższym osiedlu, średnia odległość do najbliższej kolonii sępów (Tab. 1). Z pomocą komputera wybrano także 34 losowe punkty. W sytuacji, gdy wyznaczony punkt znajdował się na płaskowyżu, wybierano klif znajdujący się najbliżej. Wszystkie punkty znajdowały się około 11 km od najbliższej kolonii i innych punktów.

Wyniki badań wskazują, że klify zajęte przez sępy w porównaniu z losowo wybranymi skałami znajdują się bliżej wybrzeży, są wyższe, leżą bliżej farm hodowlanych i są lepiej chronione przed północnymi wiatrami (Tab. 2).

Analiza krokowa porównująca stanowiska gniazdowe i losowo wybrane punkty łączyła wysokość klifu, rodzaj skał, odległość od wybrzeży i farm hodowlanych w model grupujący 97.1% stanowisk gniazdowych i 88.2% losowo wybranych klifów (Tab. 3).

Analiza składowej głównej wyjaśniająca 53% zmienności analizowanych zmiennych grupowała kolonie sępów w zależności od stopnia izolacji od innych, sąsiedztwa ludzi i dystansu do pokarmu (Tab. 4).

W porównaniu z populacjami kontynentalnymi, gniazda sępów płowych na Krecie znajdowały się na wyższych skałach, bliżej wybrzeża.

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