Foraging Behaviour and Flight Characteristics of Eurasian Griffons Gyps fulvus in the Island of Crete, Greece

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Original article

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Stavros M. Xirouchakis & Giorgos Andreou

We studied the foraging behaviour of Eurasian griffons *Gyps fulvus* on the island of Crete during 1997-2005 by direct observations in four colonies and by monitoring the movements of seven radio-equipped individuals. The estimated foraging range of griffon colonies, based on direct observations, ranged from 206-851 km^2 by using the Minimum Convex Polygon method, and 195-527 km^2 by using the Adaptive Kernel method, with corresponding means of 472 and 380 km^2, respectively. Meanwhile, radio-tracking showed that foraging vultures covered an area ranging from 390-1300 km^2. The mean foraging radius was calculated at ca 15 km and the mean maximum one at 29.9 km. On windless days, griffons' mean cross-country speed was 5.1 m/second (maximum = 13.3 m/second), with a mean climbing rate of 0.6 m/second and a mean inter-thermal gliding speed of 18.8 m/second. Any livestock carrion located up to 9 km from a colony was exploited by its members with minimum competition from individuals of adjacent areas. In total, we recorded 23 feeding incidences which took place at a mean distance of 8.4 km from the colonies. The food types identified were sheep carcasses located near stock-farms and offal disposed in waste dumps in the vicinity of the colonies. On average, the griffons allocated 7.6 hour/day to food searching. This varied significantly between months and seasons. The shortest foraging time was recorded in December (6.4 hour/day) and the longest in June (9.3 hour/day). A significant difference of one hour after sunrise was detected in the departure time from the colony between seasons revealing that griffons departed earlier during winter trying to maintain their foraging budget within the available daytime limits.

Griffon vultures *Gyps* spp. are mostly cliff-nesting raptors that breed colonially and feed gregariously sometimes forming large groups. This social lifestyle is regarded as an indirect consequence of their clumped and irregular food supply as they are almost exclusively scavengers (Houston 1979, Donázar 1993). These birds have to compete with time, because carcasses are patchily distributed and available for only a few weeks, or even a few days in hot climates, and in addition, they may be consumed by their mammalian competitors (Kruuk 1972, Houston 1974, 1976, Mundy et al. 1992). Being dependent on such an unpredictable and ephemeral food supply, griffons have to travel extensively and cooperate in order to forage successfully. Birds generally disperse over sizeable areas and scan the landscape while simultaneously watching each other's behaviour (Houston 1974). In the same context, they congregate in communal roosts which are supposed to be used for exchange of information on good feeding

grounds (Ward & Zahavi 1973). Their foraging activity is greatly facilitated by their soaring flight which minimises the energetic costs of food searching and enables them to extend their feeding range (Pennycuick 1972, 1979, Mundy et al. 1992, Houston 2001).

Research on the foraging behaviour and feeding ecology of griffon vultures has been directed towards food searching techniques (Houston 1974, Pennycuick 1983), foraging time in relation to breeding strategies (Prinzinger et al. 2002, Ruxton & Houston 2002), foraging habitat selection (Bögel 1999) and range size and movements (Elósegui & Elósegui 1977, Pennycuick 1983, Robertson & Boshoff 1986, Bahat et al. 2001). Studies on the foraging behaviour of the Eurasian griffons *Gyps fulvus* are comparatively few (König 1974, Bahat & Kaplan 1995, Bögel 1999, Bahat 2007) although the species is rather common in the western Palearctic (Birdlife International 2004), and well adapted to the rural activities of man (Cramp & Simmons 1980, Houston 1996).

Crete (8,261 km^2) holds the largest insular griffon population worldwide numbering ca 140 breeding pairs concentrated in 23 nesting colonies (Xirouchakis & Mylonas 2005). The species represents a characteristic case of long standing cohabitation with man as it has depended on livestock (i.e. sheep and goat) carcasses for food for thousands of years (Xirouchakis 2005). Not surprisingly the griffons' distribution overlaps with regions of stock raising activity that spread over ca 5,500 km^2 (67%). The vultures forage predominately over open areas with bare rocks and Mediterranean scrubland. These sites have traditionally been used as rangelands and cover 64% of the island (CORINE Land Cover database, Moss et al. 1990). The garrigues or phrygana, a characteristic Mediterranean formation of

low sclerophyllous shrubs, constitutes the main vegetation type of the Cretan pastures (35.5%) extending from the coast up to 800 m a.s.l (Papanastasis et al. 1990). However, during the last two decades, their distribution has shrunk substantially in the lowlands (0-300 m a.s.l) due to urban development and agriculture (i.e. vineyards and olive grooves). So, at present, the main sheep farming areas (as well as the griffons' foraging range) cover the phrygana and the borders of cultivation where patches of natural vegetation still occur (Kypriotakis et al. 1996, Fig. 1). Following a dramatic increase in the last two decades attributable to the EU subsidy policy, stock numbers of sheep and goat for the entire island of Crete have at present reached 1.5 million (National Statistical Service 2001). About 86% of these animals are bred in semi-mountainous and upland communities (400-1100 m a.s.l) and 77% consist of transhumant flocks (National Statistical Service 2001) that are kept in pens inside large enclosures and supported with fodder during late autumn to early spring. For the rest of the year they range freely in the uplands (>800 m a.s.l.). Annual stock mortality ranges from 1.5-3% (Veterinary Services pers. comm.), but carcasses are not equally distributed in space or time. In the wintering areas, dead animals and offal are usually thrown away in tips close to the stock yards or in the nearest small ravine or in waste dumps near the villages. In summer, domestic animals die in the field and are left in the open. Following the seasonally moving livestock, griffons forage in semi-mountainous areas (300-800 m a.s.l.) close to their breeding colonies during winter, but shift to mountainous and alpine areas (800-2,450 m a.s.l.) residing in communal roosts during summer (Xirouchakis & Mylonas 2004, Xirouchakis 2007). Thus the birds modify their foraging behaviour according to the spatial

Figure 1. Vegetation map of Crete (adopted by Kypriotakis et al. 1996). Winter pastures and sheep farming areas encompass cultivation and phrygana, maquis and oak forests. Summer pastures extend over phrygana, maquis, forests and subalpine shrubland.

and temporal distribution of the food and most probably to seasonal daytime differences in an effort to maintain sufficient food encounter rates.

Given that the foraging techniques may vary in respect to population density and contribute to population regulation through intra-specific competition (Sillett et al. 2004, Dobbs et al. 2007), the study of the griffons' foraging patterns could give us an insight into their competitive behaviour and colony interactions (Bosé & Sarazzin 2007). Further, the measurement of the foraging time budget could provide an indirect index of their seasonal food availability (Hutto 1990, Lovette & Holmes 1995), and increase our understanding of the forces controlling the foraging behaviour of the species. This could improve our conservation actions through the proper management of feeding areas and food resources. Bearing these in mind, the aim of our study was to 1) investigate the foraging behaviour of griffon vultures during the period of high colony occupancy (i.e. November-April), 2) estimate their foraging range and make comparisons with populations in continental areas, and 3) assess the daily time they allocate to searching for food.

Material and methods

Study area
We studied four griffon colonies (A, B, C, D) during the breeding season 1997-1998 (Fig. 2). These colonies were selected so as to meet certain criteria, namely: a certain degree of isolation from other colonies, a relatively large colony size, and a location where favourable flight conditions could be assumed, i.e. near hilly countryside. More specifically, the mean nearest neighbour-colony distance was 17 km (range: 13.8-23.6) which is considerably larger than the mean of 10.3 km for the island (Xirouchakis & Mylonas 2004). The mean number of individuals and egg-laying pairs per colony was 23 ± 5 (range: 14-28) and 6 ± 4 (range: 1-9), respectively, which were larger than the island means of 14 ± 0.9 individuals and 3.7 ± 0.6 egg-laying pairs per colony (Xirouchakis & Mylonas 2005). Nests and roosts were situated on vertical limestone cliffs at an altitude that ranged from 200-550 m. Mean values for the period 1990-2000 (Region of Crete 2000) showed that all study colonies annually received 760-1260 mm of precipitation. The driest period was July-August ($\bar{x} = 0.2$ mm, range: 0-11.8) and the wettest December-March ($\bar{x} = 396.5$ mm, range: 230-690). Annual temperature ranged from 17.6-18.8°C with July being the warmest month ($\bar{x} = 26.1$°C) and January-February being the coldest period ($\bar{x} = 11.1$°C). Sunshine lasted less than 6 hour/day from November till March and ranged from 6-12 hour/day for the rest of the year. Study colonies A, C and D were located in the cliff walls of gorges and were protected against the wind. Colony B was located on the southwest cliff face of a small mountain and was exposed to north-northwest winds.
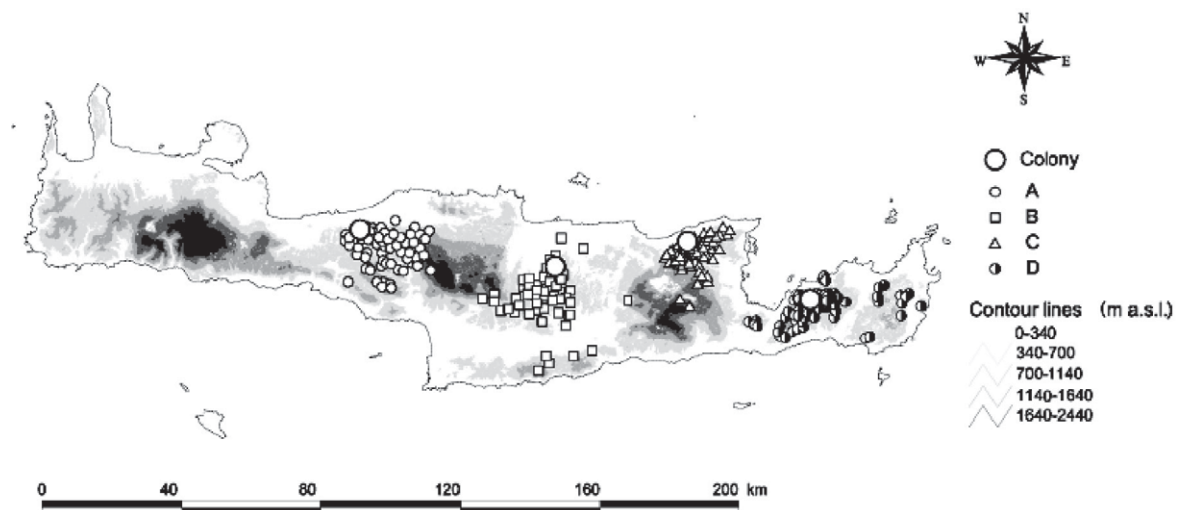

Figure 2. Foraging range of four griffon colonies (dotted circles) in Crete based on direct observations of vulture groups (≥ 5 individuals) circling in thermals (other symbols).

Fieldwork

During the period of December 1997- March 1998, when griffon colonies were occupied by vultures of variable breeding status (Xirouchakis 2007), we monitored all study colonies 2-3 times per month (43 field days, in total). More specifically, we wanted to document: 1) the area around the colony where a 'network' of foraging griffons would expand, and 2) at which distance from the colony they would mix with members of adjacent colonies. Observations were initiated at 07:30 am before the birds departed in search of food. In the first six weeks, griffons were followed by car (Rabenold 1987). All foraging groups one kilometer apart heading in the same direction were considered to be of the same origin (Rabenold 1983, Prior 1990). In this way, the flight routes and the location of the foraging areas were assessed. In addition, the main spots near the colonies (3-5 km) where birds regularly climbed in thermals were detected and noted on 1:100,000 scale maps (Hellenic Military Geographical Service). In the subsequent ten weeks, the birds were monitored from predetermined vantage points (i.e. tops of prominent hills or mountain areas) which had good visibility over both the colonies and the foraging areas. As a sampling unit, we defined arbitrarily a vulture group of up to five individuals soaring in the same thermal. Sampling units were scanned (with the aid of 10×50 binoculars and a 20×60 spotting scope) in all directions (scan sampling, Bateson & Martin 1990) and every 20 minutes, the position of the most distant one from the colony was marked on a 1:50,000 scale map (Hellenic Military Geographical Service). The distance from the colony was estimated by identifying landmarks or landscape features over which the group of vultures performed thermal circling on the map (i.e. hill tops, rocky outcrops, gorges, small plateaus, waste dumps, country churches and villages). In some cases, the exact location of soaring birds or their origin was uncertain. Such observations were eliminated. Normally, fieldwork terminated after 2.5-3 hours as birds from different colonies intermixed. Overall, we obtained a series of 7-9 location data points per field day. Additional observations were made opportunistically during the winter of 1999 focussing on the flight behaviour of foraging griffons. Flight speeds were calculated by the distance and the time elapsed between successive locations (Benvenuti et al. 1998, Weimerskirch et al. 2006) near the colonies where vultures frequently performed thermal circling. The average cross-country speed of soaring vultures was found by dividing the distance between points covered by the birds by the total time spent in thermal climbing and then gliding (Pennycuick 1972). The elevation of flight and the vertical distance traversed in a thermal was calculated trigonometrically by the horizontal distance and the angle from the observer's position (Estrella 1994). The climbing rate was calculated by dividing the vertical distance covered by soaring griffons by the time difference from the moment the first individual started to circle in the base of the thermal to the moment the first one left its top (Leshem & Yom-Tov 1996). In all observations, distance from the observer (<2.5 km), time and angle measurements were made with a laser rangefinder (LRM-2500, Newcon Optik Inc., Canada), a stopwatch (Casio HS-30W) and a clinometer (Suunto Finland, Forestry Suppliers Inc., USA), respectively. Fieldwork was pursued during warm and calm days (wind force: 0-3 Beaufort scale) as vultures largely use thermals for flight (Pennycuick 1973), therefore, their foraging behaviour would be typical for fine weather. In case the birds landed, we examined the site at the end of the field day for signs of food consumption (Coleman & Fraser 1987).

Between November 2001 and November 2002, we carried out daylong observations at the site of colony B (N=90) in an effort to estimate the time vultures allocated to food searching. The time between the departure and the arrival of the first and the last vulture at the colony was considered to be their potential foraging time. The time the majority of the birds ($>75\%$) was away from the colony was defined as the actual duration of a foraging sortie (Boshoff et al. 1984, Robertson & Boshoff 1986, Hiraldo & Donázar 1990). Mean monthly daytime was calculated from the civilian twilight sunrise and sunset times of the Astronomical Application Department/US Naval Observatory (Available at: http://aa.usno.navy.mil/) for the geographical position of the colony that particular year.

In the winter of 2003, we tried to capture adult griffons near the study colonies. We used cage-traps baited with carcasses and decoy birds (Iezekiel et al. 2003). Unfortunately, all the attempts proved unsuccessful. For this reason, in October 2004 and 2005, we used radio-tracking on eight griffons that had been recovered with symptoms of poisoning in the surroundings of colony B. The birds were subadults, as judged by plumage characteristics (Forsman 1999), so they were considered to be resident. Griffons were equipped with VHF transmitters

(BioTrack Inc., UK) weighing 55 g, attached with a Y-type backpack harness made of a 5-mm diameter silicon string (Kenward 1987, Buehler et al. 1995). The transmitters had a life expectancy of over a year and a detection range of 30-35 km in line of sight. All the marked birds were released in colony B and their presence at the colony site was checked every other day before sunset. In case they were located there, we tracked them continuously the next day. The birds were tracked using a hand-held receiver (Communication Specialists, USA) and an omnidirectional whip car antenna. We then followed the peak signal by using a directional three-element Yagi antenna until visual contact was possible (homing, White & Garrot 1990). A maximum of three radio-locations were acquired per tagged griffon per field day (i.e. every 2.5 hours starting from their departure) and these were noted on a 1:100,000 scale map. This methodology was pursued in an attempt to reduce autocorrelation, to attain an adequate sample size for analysis and in the meantime to allow homing. The minimum number of points for the estimation of foraging range size was set at 30 radio-locations per bird (Samuel et al. 1985, Aebischer et al. 1993, Seaman et al. 1999). All tagged birds were tracked on a weekly basis (2-3 times) until mid April when griffons abandoned the colonies and resided in communal roosts in the uplands.

Data analysis

We compared the observed flight characteristics of griffons to corresponding values computed by the program FLIGHT 1.18 (Pennycuick 2007). More specifically, we calculated the forward speed at which minimum sink is achieved (minimum sink speed V_{ms}) and the forward speed at which its ratio to sink is maximised (best glide speed V_{bg}). These parameters are equivalent to the minimum power speed (V_{mp}) and maximum range speed (V_{mr}) of flapping flight, respectively (Pennycuick 1989). Furthermore, we computed the optimal inter-thermal and cross-country speeds by climbing in thermals at the observed rate. The body drag coefficient $C_{D,par}$ was set at 0.1 (Pennycuick et al. 1996) and the air density was set in accordance with the observed mean altitude of thermal-circling griffons. Aerodynamic calculations were based on the biometrical data described for the species in Crete: body mass (7.6 kg, N = 92), wing span, i.e. the distance between the extended wing tips measured by keeping the bird on its back with the wings fully outstretched (2.56 m, N = 97), and wing area, i.e. the average wingspan

multiplied by the average wing width (0.88 m^2, N = 19) (Xirouchakis & Poulakakis 2008).

We digitised all observation points and radio-locations using Geographic Information System (ARC/VIEW 3.2, ESRI 1996) and calculated respective positions in UTM coordinates of the Hellenic Geodetic Reference System. The mapping of the foraging range of each study colony was generated using the CALHOME program and its default smoothing parameter with a 30 × 30 cell-grid size (Kie et al. 1994). We applied the minimum convex polygon (MCP 100%, Mohr 1947) for purpose of comparison with the existing literature and the 50%, 75%, 90% and 95% probability contours of the Adaptive Kernel (ADK) estimator (Worton 1989,1995), which is not affected by the scale or the grid size of the map (Harris et al. 1990, Kie et al. 1996, Lawson & Rodgers 1997).

The foraging range (based upon radio-locations) of instrumented birds was computed by the MCP100%, ADK95% and the BIN95% (bivariate normal, Jennrich & Turner 1969) which assumes random movement but with decreasing probability away from the colony (central-place foraging, Rosenberg & McKelvey 1999). The minimum distance covered by the birds per day was calculated theoretically by their movement between successive fixes. A complete foraging sortie was recorded when a radio-tagged bird left and returned to colony B in the same day. In cases in which the bird overnighted in an adjacent colony or in a communal roost, the radio-locations were discarded from the analysis in order to reduce bias.

In an effort to detect differences in the species' foraging time budget, we divided the year into two periods, winter (15/11-14/4) and summer (15/4-14/11) (Xirouchakis & Mylonas 2004). Additionally, we partitioned the annual cycle into a non-breeding period (August-November) and a breeding period (December-July). The latter was further divided into the egg-laying/incubation stage (i.e. December-February) and the egg hatching/chick rearing stage up to fledging (i.e. March-July) (Xirouchakis & Mylonas 2007).

The Kolmogorov-Smirnov test was used for testing the normality of the data. In case the assumption of normality was violated, comparisons of means were made by the non-parametric Kruskal-Wallis and Mann-Whitney tests. The distribution of all radio-locations in relation to the colony was tested by the Rao's spacing test, while significant differences between birds were checked by the

Watson-Williams F-test. All statistical analyses are described in Zar (1996) and Mardia & Jupp (2000) and were conducted at a 0.05 level of significance by the use of SPSS 15.0 (Norusis 2006) and Oriana 2.02 (Kovach Computing Services 2005).

Results

Foraging behaviour
In all morning observations, griffons left the colonies in one large group (> 70% of the birds). Normally they circled in front of the cliffs ($\bar{x} = 7 \pm 5.6$ minutes, range: 0-30 minutes, N = 61) before entering the nearest thermal. After the first 2-3 thermals, the initial group was divided and griffons followed different routes leaving each thermal one by one. However, their overall flight pattern demonstrated a directional trend apparently towards their foraging areas (see Fig. 2).

The elevation of soaring griffons above the ground ranged from 96-440 m ($\bar{x} = 248 \pm 112.3$ m). The mean climbing rate in thermals was 0.6 m/second whereas the time spent in thermal circling ranged from 3-22 minutes ($\bar{x} = 8 \pm 6.9$ minutes). The inter-thermal gliding speed was determined at 18.8 m/second. The mean cross-country speed was calculated at 5.1 m/second or 18.4 km/hour (maximum = 47.9 km/hour, Table 1) though a 'sinking' individual heading towards others over food could accomplish a flying speed of ca 50 m/second (180 km/hour). Considering that the flight type of a Eurasian griffon is 58% gliding and 30% thermal circling (Spaar 1997) the 'true' cross-country speed was estimated at 12.6 m/second (45 km/hour). The bird flight software computed a forward speed of 9.9 m/second (V_{ms}) for a minimum downward speed (sink rate) of 0.8 m/second and a best gliding speed of 15.6 m/second. Moreover, with a mean climb rate of 0.5 m/second, it predicted a maximum cross-country speed of 5.3 m/second, achieved by an optimal inter-thermal speed of 18.8 m/second, or 5.1 m/second by flying between thermals at the best glide speed (V_{bg}).

Feeding incidences were observed on 23 occasions. The main clue to griffons having located food was soaring low over the ground (< 100 m) or 'sinking' with hanging feet or directional flapping flight. In 19 cases, the food consisted of sheep carcasses while in the rest, it was offal and by-products of slaughterhouses disposed off in waste dumps. Nine of the carcasses were located inside stock yards or in pits outside the fencing. The mean distance of the feeding sites from the colonies was 8.4 km (range: 2-19.6 km). The majority (74%) of the feeding bouts took place before 12:00 am (median time = 10:30 am, range: 07:05 am-15:22 pm). The time of feeding and the distance of feeding sites from the colonies was positively correlated r = 0.73, P < 0.001. On two occasions, we have reason to believe that vultures from adjacent colonies were attracted to the same carcass. In both cases, birds roosted overnight in a rocky outcrop near the food and consumed it early in the morning (7:00 am) the next day.

Foraging range
The mean foraging range of griffon colonies, based on direct observations, was estimated at ca 472 km^2 (range: 291-851 km^2) by the MCP100% and 380 km^2 (range: 195-527 km^2) by the ADK95% estimators, respectively (Table 2). The MCP100% method indicated that griffons foraged on average at a distance of 12 km (range: 8.1-16.5 km) from the colonies (see Table 2, see Fig. 2). Focal vulture groups joined birds from adjacent colonies at a mean distance of 9.4 km from the colony (range: 6.8-11.6 km, N = 156). The foraging range did not depend on the colony size, i.e. number of individuals (r = -0.42,

Table 1. Flight characteristics of griffon vultures in Crete. N = number of observations.

Flight characteristics	Mean ± SD	Minimum	Maximum	N
Climb rate in thermals (m/second)	0.6 ± 0.38	0.16	1.14	26
Duration of thermal soaring (minutes)	8 ± 6.9	3	22	26
Starting height of thermal soaring (m)[1]	248 ± 112.3	96	440	26
Inter-thermal gliding speed (m/second)	18.8 ± 9.26	6.7	36.7	28
Duration of inter-thermal gliding (minutes)	3.5 ± 1.7	1	7	28
Cross-country speed (m/second)	5.1 ± 4.4	0.6	13.3	24
Cross-country phase duration[2] (minutes)	14.3 ± 7.1	7	30	24
Group size	13 ± 7	3	33	47

[1]Mean altitude of the observer's position: 340 m.

[2]Thermal soaring plus inter-thermal gliding.

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Table 2. Foraging range (km^2) and mean foraging radius (km) of four griffon colonies in Crete estimated by the Adaptive Kernel (ADK) method, with a 30×30 grid cell density, and the minimum convex polygon (MCP) methods. N = number of observations of focal vulture groups.

Colony	N	MCP 100%	ADK 50% (N)	ADK 75% (N)	ADK 90% (N)	ADK 95% (N)
A	80	291.5	70.6 (40)	181.4 (60)	249.5 (72)	319.6 (76)
B	55	850.6	86.1 (28)	201.1 (41)	406.9 (50)	478.2 (52)
C	78	206.0	45.9 (39)	93.2 (59)	169.8 (70)	194.8 (74)
D	96	538.8	54.7 (48)	171.7 (72)	448.7 (86)	527.1 (91)
Mean	77	471.7	64.3	161.8	318.7	379.9
Mean radius (range)		12.3 (8.1-16.5)	4.5 (3.8-5.2)	7.2 (5.4-8)	10.1 (7.4-12)	11 (7.9-13)

$P > 0.05$) nor the mean distance from the neighbouring colonies ($r = -0.11$, $P > 0.05$). However, a comparison between the foraging range and the total number of individuals residing in the nearest colonies suggested a positive relationship, but this was not significant.

One radio-tagged griffon remained in the vicinity of the release colony for just 22 hours and was never resighted. The remaining seven griffons were tracked for 554 field-days during October-April 2004-2005 and generated a total of 957 radio-locations. Our data analyses were restricted to cases where equipped individuals performed complete foraging trips, i.e. departed and arrived at the colony during the same day. This meant that only 40% of the field-days (range: 22.2-70.8%) were taken into account with 513 radio-locations.

By pooling data from all birds, the respective MCP100% range size was estimated at 1278 km^2 (radius = 20 km). However, the mean MCP100% of all fixes for each bird created a foraging range of 660 km^2 (Table 3, Fig. 3). Similarly, according to the ADK95% and BIN95% probability contours, the mean foraging range was 692 ± 299 km^2 and 838 ± 302 km^2, respectively (range: 387-1385 km^2, see Table 3). The foraging range size estimated by radio tracking (MCP100%, ADK95%) was 31.7-54.6% larger than the corresponding estimates derived from direct observations. The mean foraging radius of a hypothetical circular foraging range estimated by all birds and methods was 14.9 km (range: 11.2-20.4 km). Similarly, the average maximum foraging distance was found to be 29.9 km from the colony (range: 17.4-47.5 km), while the minimum total distance travelled by radio-tagged birds was 24.7 ± 4.6 km per field day (range: 17.6-30.3 km).

The overlap of foraging ranges (MCP100%) between radio-tagged birds was $24.3 \pm 12.3\%$ (range: 11.1-44.3%), while the pattern of spatial use showed that this was not at random (Rao's spacing test $U = 241.6$, $P < 0.01$; see Fig. 3). On average, 75% of the radio-locations were contained within $31.6 \pm 6.42\%$ of the foraging range estimated by the ADK95% method. The familiarity of the radio-tagged birds with the main feeding areas was notable. Birds visited the same places sometimes day after day. Radio-locations were packed in two main areas, i.e. the farmland around the colony where livestock was kept in stockyards and the nearest massif to the south of the colony (see Fig. 3). No significant differences were detected in the mean flight direction of radio-tagged birds when foraging

Table 3. Foraging range (km^2) and hypothetical circular foraging radius (km) (in brackets) of seven griffon vultures radio-tracked in Crete during October-April (2004-2005) as estimated by Adaptive Kernel (ADK95%), the Bivariate Normal (BIN95%) and the minimum convex polygon (MCP100%) methods. D_1 = Mean inter-radio location distance (km), D_2 = Maximum distance (km) from the colony.

| Vulture ID	No. of days		No. of radio fixes		ADK 95%	BIN 95%	MCP 100%	D_1	D_2
	Tracked	Detected	Total	Sample					
26	34	28	68	35	581.1 (13.6)	675 (14.7)	393.4 (11.2)	6.8	26.2
06	150	117	234	76	781.5 (15.8)	953.8 (17.4)	1012 (18)	9.1	31.0
10	87	77	154	112	1309 (20.4)	1385 (21)	1157 (19.2)	10.2	47.5
31	24	24	51	48	386.6 (11.1)	456.2 (12.1)	289.2 (9.6)	5.6	17.4
37	63	9	119	72	669.7 (14.6)	919.8 (17.1)	687 (14.8)	7.2	28.4
51	97	92	175	79	499.4 (12.6)	604.1 (13.9)	394.4 (11.2)	7.8	30.2
60	99	78	156	91	615.3 (14)	871.2 (16.7)	687.1 (14.8)	7.8	28.7
Mean	79	67	137	73	692 (14.6)	837.9 (16.1)	660 (14.1)	7.8	29.9
Total	554	470	957	513					
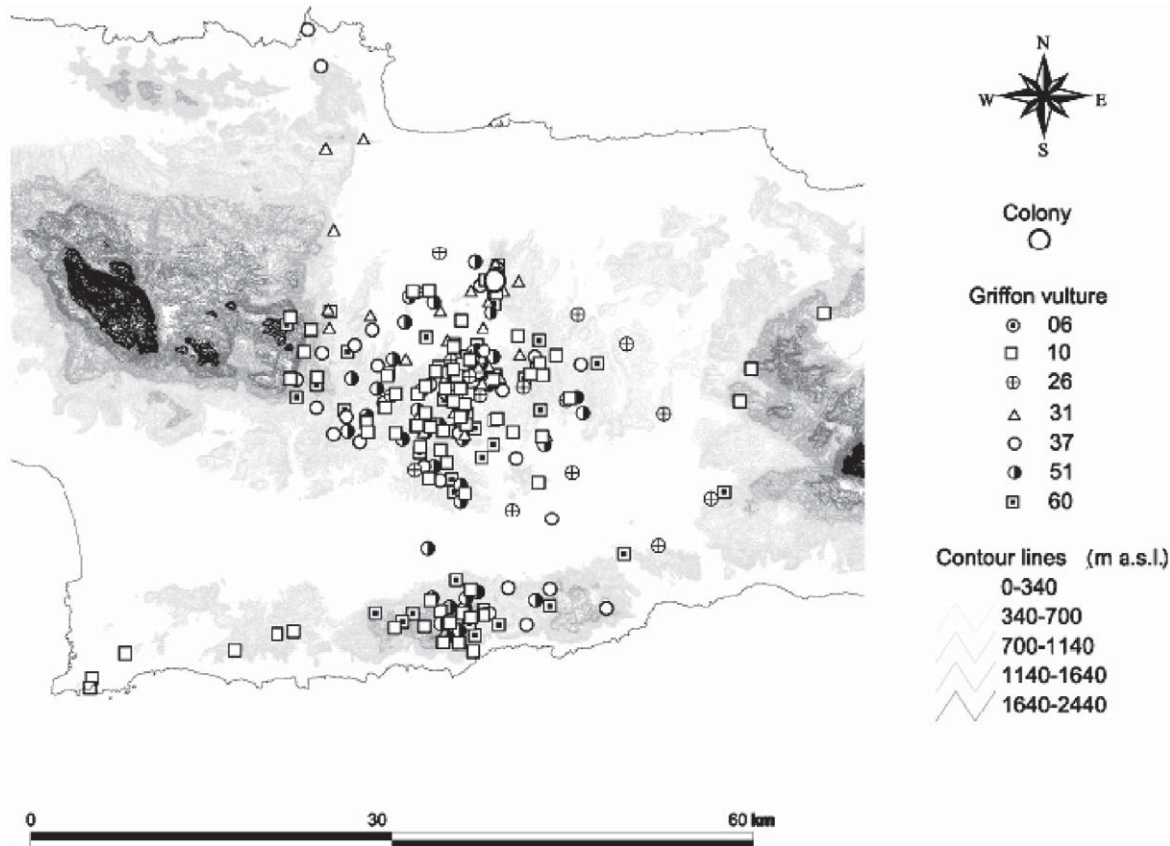
Figure 3. Foraging range of a griffon vulture colony in Crete based on radio-tracking of seven sub-adult individuals. The symbols denote radio-locations acquired during October-April 2004, 2005.

($\bar{x} \pm$ angular deviation $= 203 \pm 39.6°$, range: 180.7-230.3°, Watson-Williams F-test: $F = 3.89$, $P = 0.09$).

Foraging time budget

Our data show that on average 9 hours/day could potentially be allocated to food searching (Fig. 4).

This varied seasonally; the minimum time available was recorded in December (8.2 hours) and the maximum in July (10.2 hours). However, the actual foraging time was on average shorter by more than one hour ($\bar{x} = 7.6 \pm 1.1$ hour/day) and varied significantly between months ($F_{11,73} = 5.7$, $P < 0.001$)
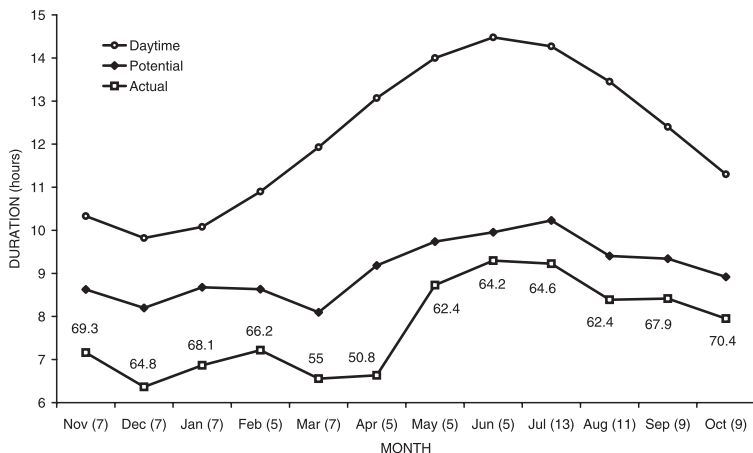

Figure 4. Monthly means of daylight hours and potential and actual hours of foraging (also shown as % of daylight hours) of griffon vultures in Crete estimated by daylong observations at one colony. Monthly sample sizes are shown in parentheses. Winter: November-April and Summer: May-October.

Figure 5. Time differences between the sunrise and the departure of griffon vultures (filled circles and unbroken lines) and between arrival and sunset (open circles and broken lines) in one colony in Crete. Winter: November-April and Summer: May-October.
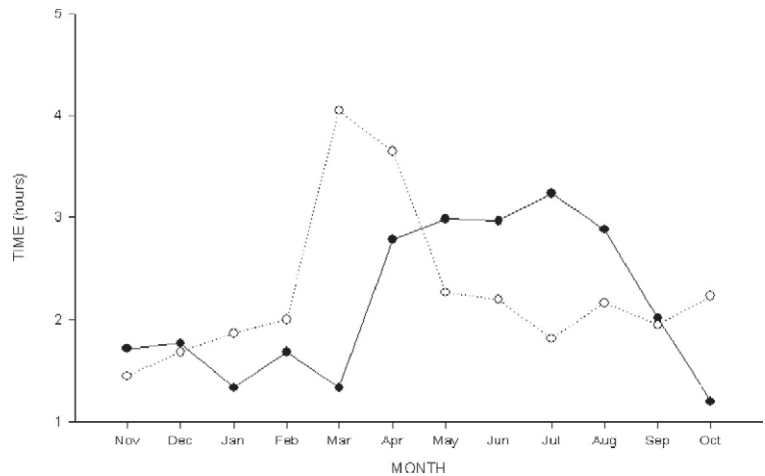
and among seasons ($\bar{x}_{winter} = 6.8 \pm 0.37$ hour/day, range: 6.3-7.2 hour/day, $\bar{x}_{summer} = 8.4 \pm 0.90$ hour/day, range: 6.6-9.3 hour/day, $t_{10} = 3.56$, $P < 0.01$). The shortest foraging time was recorded in December (6.4 hour/day) and increased progressively onwards peaking in June (9.3 hour/day). This pattern was probably an effect of a covariance with the length of the daylight period ($r = 0.77$, $P < 0.01$, see Fig. 4) as the percentage of daytime allocated to food searching was on average similar between seasons (winter: 64.7% vs summer: 63.2%, Mann-Whitney $U = 12$, $P = 0.37$). Overall, the potential and actual foraging times showed similar annual fluctuations, but their difference was not constant. These differences were short during the summer and autumn (a minimum of 40 minutes in June) and longer during the winter and spring (a maximum of 108 minutes in December) while the average for the year was $\bar{x} = 80 \pm 32.2$ minutes. The difference in the duration of foraging sorties between the breeding and the non-breeding period was not significant ($\bar{x}_{breeding\ period} = 8.1 \pm 1.2$ hour/day, $\bar{x}_{non\text{-}breeding\ period} = 7.6 \pm 1.61$ hour/day, $t_{88} = 0.98$, $P > 0.05$). However, within the breeding period, birds spent less time on food searching during incubation than during the chick-rearing stage ($\bar{x}_{incubation} = 6.8 \pm 1.38$ hour/day, $\bar{x}_{chick\text{-}rearing} = 8.3 \pm 1.48$ hour/day, Mann-Whitney $U = 134.5$, $P \ll 0.001$).

A significant seasonal variation was also observed in the vultures' departure time with respect to sunrise (Fig. 5). The time when the birds left the colony occurred 1.57 ± 0.22 hour (range: 1.33-1.77 hours) after sunrise in winter and 2.58 ± 0.72 hours (range: 1.2-3.23 hours) after sunrise in summer ($t_{10} = 3$, $P = 0.013$). Such a difference was not observed in the timing of their return. The birds returned to the

colony ca 2.3 hours before sunset throughout the year ($\bar{x}_{winter} = 2.21 \pm 1.05$ hours, range: 1.45-4.05 hours vs $\bar{x}_{summer} = 2.33 \pm 0.61$ hours, range: 1.82-3.65 hours, $t_{10} = 0.2$, $P = 0.81$). Similarly, no significant differences were detected for departure and arrival times (t-tests, $P > 0.05$) neither between the breeding and the non-breeding period, nor between the incubation and the chick rearing period.

Discussion

The flight speeds of griffons recorded in Crete were similar to figures determined by the flight mechanical theory (Pennycuick 1989), or estimated in the field, in some cases by using more sophisticated techniques, e.g. tracking by motor-gliders or radars (Cape griffon *Gyps coprotheres*: 18-20 m/second, Van der Plaat 1946; Rüppell's griffon *Gyps rueppellii*: 13 m/second, Pennycuick 1972; Eurasian griffon: 12.2 m/second, Spaar 1997). Foraging griffons in the plains of Serengeti (east Africa) fly at similar speed, i.e. up to 18 m/second but at a greater height above the ground (800 m; Pennycuick 1972), which might be due to the weather conditions when the data were collected, i.e. a high cloudbase and strong thermals created during the dry seasons. The climbing rate of a soaring griffon in Crete was lower than the figures reported in the literature, e.g. ≥ 3 m/second in the Alps (Bögel 1999), 1.84 m/second in Israel (Spaar 1997), and up to 5 m/second in East Africa (Pennycuick 1972). Apart from species-specific biometrics and aeronautic characteristics (e.g. aspect ratio and wing span), these differences could be attributed to differences in field techniques, observation period, altitude, topographic

and atmospheric conditions (e.g. migration period, midday sightings, dynamic slope soaring, air density or wind speed), or to local climatic effects (e.g. high ground temperature) that produce rising air currents some of which are rarely recorded on Crete (e.g. 'dust devils', Pennycuick 1972, Kerlinger & Gauthreaux 1985, Kerlinger 1989). Similarly, the altitude of flight, which is related to the climbing rate in thermals, was consistent with other studies only for morning and early midday hours when the creation of thermals is limited (Pennycuick 1972, Kerlinger 1989, Spaar 1995, Spaar & Bruderer 1996). Overall, the griffons seemed to adapt their flight activities according to the local flight conditions looking for suitable thermal updrafts. In general, they pursued cross-country trips by flying at the best glide speed between thermals. In this way, they could maximise the distance covered for every meter of height loss and perform more prolonged glides before needing another thermal to move on (Pennycuick 1989, Spaar & Bruderer 1997).

The size of a feeding area occupied by a group of birds has been reported to vary in relation to their body size and food density (Schoener 1968,1981). Additionally, interactions of foraging habitat availability, food abundance, energetics and territoriality are known to influence the size and the use of the landscape (Newton 1979, Bloom et al. 1993, Babcock 1995, Bennet & Bloom 2005). In the present case any carrion located up to a distance of 9 km from a colony was easily exploited by its members with minimum competition by vultures from adjacent colonies. This figure matches the mean nearest neighbour-colony distance recorded on the island (i.e. 10.3 km; Xirouchakis & Mylonas 2004). So although griffons did not show any behavioural resistance to the expansion of foraging by birds from neighbouring colonies, they competed for resources by quick exploitation. This minimum area around each colony could be described as a 'feeding territory' in the traditional sense (Pitelka 1959) being primarily exploited by its occupants (Krebs & Davis 1991). On the other hand, the foraging range depended largely on the distance of the colony from the food sources. The foraging range size estimated in the present study is consistent with other mainland griffon populations which feed largely on livestock carrion (25-70 km, Glutz et al. 1971, König 1974, Elósegui & Elósegui 1977). Foraging ranges of 930-8,695 km^2 (radius = 17.2-52.6 km) have been reported in Spain (Arroyo & Garza 1996), 620-1,383 km^2 (radius = 14.5-20.9 km) in Israel (Bahat & Kaplan

1995, Bahat 2007), 150 km^2 (radius = 6.9 km) in the Austrian Alps (Bögel 1999) and 6-15 km away from the colony for the Cape griffon in South Africa (Boshoff et al. 1984). Similar foraging ranges have also been reported for other vulture species that are central foragers or inhabit rural regions (Bearded vulture *Gypaetus barbatus*: 15-20 km, Brown 1988, Margalida & Garcia 2002; Eurasian black vulture *Aegypius monachus*: 17-28 km, Carrete & Donázar 2005, Vasilakis et al. 2006). In contrast to this, East Africa breeding Rüppell's griffons may travel 140-150 km daily in order to forage successfully (Houston 1976, Pennycuick 1983) though a normal trip to the nearest concentration of wild ungulates is about 75 km (Pennycuick 1972).

The fact that the radio-tracked birds were individuals that had been rehabilitated after poisoning might be criticised on the grounds that they were young and possibly inexperienced. We argue that these birds were most likely poisoned due to their experience in finding food and/or their dominance over carcasses, thus we regard the data obtained as valid. We also believe that these birds revealed the full spectrum of the colony's feeding range as non-breeding individuals, not attached to nest sites, forage at greater distance than breeders (Meretsky & Snyder 1992, Bahat & Kaplan 1995, Carrete & Donázar 2005, Vasilakis et al. 2006). In similar cases, rehabilitated griffons have been reported representative of the species foraging and feeding behaviour (Boshoff et al. 1984).

The daily energy expenditures (E_d, kJ/day) and the foraging rate (F_r, kJ/hour) in birds can be expressed by allometric equations of body mass (M) namely $E_d = 10.4M^{0.67}$ (data form 82 bird species, Nagy 1987, Nagy & Obst 1991) and $F_r = 2.02M^{0.68}$ (data from 67 bird species, Bryant & Westerterp 1980). So theoretically, the minimum number of hours a bird should forage per day (i.e. foraging budget) could be given by the ratio E_d/F_r, which is at least five hours regardless of its body mass (Maurer 1996). In the present study, the time spent by foraging griffons was always longer, i.e. 7.6 hours (ca 64% of the daytime). Comparable figures have been reported by Leconte (1977) who estimated that the species forages for 7-8 hours per day (which corresponds to 58.3-66.6% of the mean daylight period), two additional hours (11.7%) for preening and the remaining daytime (20.8%) for resting. Likewise, long foraging times have been recorded, with respect to daylight hours, for other large vulture species such as the bearded vulture (77%, Brown

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1988) and the Eurasian black vulture (68.8-87.5%, Donázar 1993).

The foraging budget of griffons depended on the daytime hours which determined the maximum time available for foraging as well as the flying and soaring conditions. Birds had to intensify their prospecting effort during the period of low food availability (winter) and combat unfavorable weather conditions such as fog or rain that impede thermal creation. As a result, birds departed from the colony one hour earlier in winter compared to summer in order to keep their foraging budget within the available daytime limits. In some cases, they were also helped by suitable air currents which facilitated their earlier departure. Similar foraging patterns where birds try to maximise their foraging budget in winter have been reported in many large raptors that depend on thermals for their movements, e.g. the Californian condor *Gymnogyps californianus*, the African fish-eagle *Haliaetus vocifer*, the Rüppell's vulture, the African white-backed griffon *Gyps africanus* and the Eurasian black vulture (Koford 1966, Thiollay 1981, Houston 1983, Brown 1988, Hiraldo & Donázar 1990). The Cape griffon is an exception to this rule as the departure time relative to sunrise is delayed in the winter compared to the summer (Robertson 1983, Boshoff et al. 1984). This difference is due to the weather conditions and the farming practices near its colonies. Birds feed largely on resident livestock producing the highest dead biomass during winter (Robertson & Boshoff 1986, Mundy et al. 1992, Scott et al. 2000). Meanwhile, suitable flying conditions (SE winds) prevail in summer allowing the vultures to depart early in the morning (Boshoff et al. 1984). However, in the present study, griffons terminated their foraging trips almost four hours before sunset during March and April indicating that they had foraged successfully in just 55% and 50.8% of the daytime. One plausible explanation for this extreme pattern was that during these months, intra-colony competition was probably relaxed as non-breeders had abandoned the colonies (Xirouchakis 2007), and the remaining birds could achieve a higher food intake per feeding bout. Besides this, the colony was occupied largely by breeding birds which were more experienced in finding food and dominant over carcasses against younger ones. Moreover, this period coincided with the peak demand of the meat market due to the Greek-Orthodox Easter which means abundant slaughter remains in waste dumps. From late April onwards, livestock was transferred to the summer pastures and chick-rearing vultures were forced to travel greater distances and spent more time in search of food.

It could be argued that the foraging pattern of griffons was rather a product of food predictability rather than proximity to food sources since 56% of the feeding incidences took place close to the colonies in waste dumps and stock yards where food was expected to accumulate. Griffons are known to forage opportunistically and concentrate near reliable food sources (Galushin 1971, Donázar 1993, Houston 2001, Gavashelishvili & McGrady 2006). Refuse tips near stock-farms have played a crucial role for their well-being in Crete like in other Mediterranean countries (Sunyer 1992, Donázar 1992, Camiña 2002). However, in the vast majority of the cases, the existing ways of carcass disposal are in breach of the EU sanitary regulations (e.g. 1774/2002, European Union 2002). These regulations pose a serious threat to the griffons and to other avian scavengers (Tella 2001). Remedial decisions (e.g. 322/2003, European Commission 2003) have proved impractical (Camiña & Montelío 2006) and in the case of Crete, the regulation is very often broken by farmers. Artificial feeding, organised in an official way could alleviate the problem and has been excessively used in vulture conservation when food was in short supply (Heredia & Heredia 1991, Frey 1992, Sarazzin 1998, Vlachos et al. 1999, Genero 2006). However, in several cases, the long-term effectiveness of supplementary feeding has been seriously questioned (Bretagnolle et al. 2004) and the management of feeding stations has proved rather complex and sometimes producing results that were contrary to expectations (Piper 2004, Carrete et al. 2006). So as soon as the effectiveness of such management schemes is fully assessed, their implementation should also consider the species demography and bottle-neck periods as well as foraging ecology and social structure (Meretsky & Mannan 1999, Piper 2006, Bosé & Sarazzin 2007).

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