

**Modelling foraging distribution of Griffon
Vultures (*Gyps fulvus*) on the island of Crete,
Greece**

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Modelling foraging distribution of Griffon Vultures (*Gyps fulvus*) on the island of
Crete, Greece

by

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Abstract

The Griffon Vulture is an opportunistic scavenging raptor. It has a range which includes areas in Europe, Asia, North Africa and the Middle East. The European population is estimated to contain 20000 breeding pairs. Within Europe, the range is mainly distributed about the Mediterranean, and the majority of the European population is located in Spain.

Whilst once widespread in Greece, the range has now been much reduced and the population in Eastern Europe can be considered to be endangered, regardless of the large Spanish population. Crete now contains the largest and most important population in Greece with 70 - 80% of the population. Crete has the biggest viable population in the Eastern Mediterranean. In Crete the population may be more closely tied to pastoralism than in other parts of Europe, possibly leaving it vulnerable to future changes in land use. Investigation into the relationship between Griffon Vultures and their food sources is required to gain a further understanding of the possible impact future changes may have.

The food available to Griffon Vultures on Crete was initially determined using livestock census data and information from livestock owners. Modelling of the species distribution using telemetry data was then implemented under different scenarios, and the contribution of food availability to the Griffon foraging distribution was investigated. The models were implemented with 19 environmental variables, both natural and anthropogenic. Eight scenarios were modelled, being combinations of adults and juveniles, summer and winter, and with and without available food. The contribution of food resources to the foraging distribution of the Griffon Vulture modelling was performed using MAXENT, a maximum entropy model.

Food availability is significantly greater above 600m, however the food availability does not contribute more than 10% to the Griffon Vulture foraging distribution models. There is a significant difference in the Griffon Vulture foraging distance in summer versus the foraging distribution in winter. There not a significant difference between the foraging distributions of adults and juveniles. Finally, food availability is significant in modelling Griffon foraging distributions. The environmental variables which contributed the most to the models were cloud cover, annual precipitation and the distance to colonies.

Keywords: *Gyps fulvus*, species distribution modelling, Maxent, food availability.

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1. Introduction

1.1. Background and Significance

1.1.1. Understanding complex interactions

Understanding the human and natural systems on which humanity has an impact, and the inherent feedbacks prospective changes cause in these systems is a research imperative currently receiving international attention. This is due to the realisation of the negative consequences currently caused by lack of knowledge, and the requirement for further knowledge of all human and natural systems to prevent unintended consequences. The complexity of the systems being investigated means that it is unrealistic to assume that these systems can ever be completely modelled, so unforeseen outcomes may still occur. Nevertheless, the understanding gained from modelling activities is still a worthwhile pursuit so that informed and rational decisions may be made at all scales, from the local to the international level.

Crete is a particularly complex system which has undergone much recent change. Land use on the island of Crete, Greece has undergone severe changes since Greece joined the EU in 1981. One of the main impacts has been a large increase in livestock numbers due to subsidisation by the EU (Hostert, Roder, Hill, Udelhoven, & Tsioulis, 2003) (Xirouchakis & Mylonas, 2005)(Lorent, Sonnenschein, Tsiourlis, Hostert, & Lambin, 2009)). This in turn has led to an increase in grazing pressure, with up to 40% of the vegetation cover in rangeland areas undergoing degradation (Hostert, Roder, Hill, Udelhoven, & Tsioulis, 2003). Whilst an increase in livestock numbers may have led a corresponding increase in the Eurasian Griffon Vulture population, the lack of knowledge on the importance of the links between vegetation and livestock density, and also between livestock density and Griffon vulture populations indicates that the future of the Griffon vulture population is not straightforward (Hostert, Roder, Hill, Udelhoven, & Tsioulis, 2003)(Xirouchakis & Mylonas, 2005). Some of these changes outlined above have the potential to cause unforeseen negative impacts.

1.1.2. Species Distribution Modelling

Geo-information provides tools which make modelling natural systems and the interactions between spatially explicit phenomena relatively straightforward. By using these powerful tools it is possible to investigate relationships between species and their habitats. Species distribution models have been rapidly developing. These offer more powerful methods, than habitat modelling, to predict species distributions using environmental parameters, including both anthropogenic and natural variables, using statistically or theoretically derived surfaces (Guisan & Thuiller, 2005). They have also been used to investigate the relationships between species and their habitats by running the models with different under different input scenarios.

There are now many various species distribution modelling techniques available, and these calculate the distribution based on different statistical techniques. The choice of model generally reflects the available data, and choices which require presence only data are more limited. Some models which have been developed to use presence only data are BIOCLIM ((Beaumont, Hughes, & Poulsen, 2005), DOMAIN (Carpenter, Gillison, & Winter, 1993), GARP (Stockwell & Peters, 1999) and MAXENT(Phillips, Anderson, & Schapire, Maximum entropy modeling of species geographic distributions, 2006).

1.1.3. *Gyps fulvus*

The Eurasian Griffon Vulture, *Gyps fulvus*, is a cliff-nesting raptor and is exclusively an opportunistic scavenger which mainly feeds on the soft tissue of carrion (Xirouchakis and Mylonas, 2005a; Xirouchakis and Mylonas, 2005b; Xirouchakis and Mylonas, 2007; Donazar et al., 1993; Cramp and Simmons 1980; Xirouchakis, 2009; Fernandez, 1998). Although Griffon Vultures prefer larger species (Donazar et al., 1993), there are few such carcasses available in Crete due to low numbers of larger domestic species and burial of the carcasses (Xirouchakis and Mylonas 2005b). Instead, in Crete the griffon diet consists of carcasses from domestic sheep, goats and pigs with the main source of food being sheep carcasses (Xirouchakis and Mylonas 2005b). There is also one wild species of goat. However this is not a main source of food (Xirouchakis and Mylonas 2005b).

The Eurasian Griffon Vulture has a range which includes areas in Europe, Asia and North Africa and the Middle East (Birdlife International, 2004, Xirouchakis and Mylonas, 2005a, Cramp and Simmons 1980 in Xirouchakis and Mylonas 2007b, Garcia-Ripolles et al. 2005). The European population is estimated to contain 20000 breeding pairs, and within Europe the range is mainly distributed about the

Mediterranean (Xirouchakis and Mylonas 2005a, Donazar et al. 1993, Cramp and Simmons 1980). The majority of the European population is located in Spain, and this population has been increasing (Parra and Teller 2004), although at a slower rate more recently (Fernandez et al. 1998).

On the other hand, whilst once widespread in Greece, the range has now been much reduced, and the population in Eastern Europe can be considered as endangered regardless of the large Spanish population (EGVWG, 2004). A reduction in the former range is due to a reduction in transhumance, and also deliberate poisoning of Griffons (Maragilda et al., 2007). Crete now contains the largest and most important population in Greece with 70 - 80% of the population, and the biggest viable population in the Eastern Mediterranean. (Xirouchakis and Mylonas, 2005a). In Crete the population may be more closely tied to pastoralism than other parts of Europe (Xirouchakis and Mylonas, 2005a) leaving it vulnerable to future changes in land use.

The Griffon vulture is not currently a threatened species over the entire range as the species has an increasing population in Spain (Parra and Telleria, 2004). However, within Greece the species is considered vulnerable (Handrinos, 1992 in Xirouchakis and Mylonas 2005a, Xirouchakis and Mylonas 2006) and there has been considerable decline in the population in Crete since the late 1970s (Handrinos, 1985). The griffon is considered to be under the same conditions that have lead other similar species to the endangered stage (Xirouchakis and Mylonas 2005a; van Beest, van den Bremer et al. 2008, Donazar et al., 2002). There have been many studies conducted on the Griffon vulture (Emecen, 2009, Fernandez et al., 1998 Parra and Telleria, 2004 Sarrazin et al., 1996, Slotta-Bachmayr, 2004 ;van Beest et al., 2008; Xirouchakis, 2007; Xirouchakis, 2005a; Xirouchakis, 2005b Xirouchakis, 2009 ; Xirouchakis, 2006; Xirouchakis, 2005c; Xirouchakis, 2004; Xirouchakis, 2008) which all demonstrate the need to carefully monitor continuing conditions.

The Griffon Vulture breeds on cliffs and occasionally in trees. There are estimated to be 175-192 breeding pairs in Greece (Xirouchakis and Mylonas 2006), with 70 – 80% of the population in Crete (Xirouchakis and Mylonas 2005a). On Crete the population is approximately 379 individuals, with 141 breeding pairs (Xirouchakis and Mylonas 2005a). There are 23 colonies which are spread over the island. In summer the colonies inhabited are higher up in the mountains, whereas in winter colonies located on the sea cliffs are also utilised (Xirouchakis and Mylonas 2005a). The foraging range has been estimated to be up to 8km from the nesting site (Xirouchakis and Mylonas 2005; Xirouchakis 2007; Xirouchakis and Andreou

2009). The total population has been stable in recent years, although the size of individual colonies has changed significantly which may be due to changes in food availability (Xirouchakis and Mylonas 2005).

1.2. Research Problem

While there has been research into the foraging behaviour of the adult vultures during feeding (Xirouchakis and Mylonas 2007; Xirouchakis and Andreou 2009). Less is known about the differences in food sources between the juveniles and the adults. The proportion of different species in the griffon diet has been investigated (Xirouchakis and Mylonas, 2005) leading to recognition of the importance of domestic ungulates in the Griffon diet. Eurasian Griffon Vultures have shown a high degree of ecological plasticity in other studies (Margalida et al. 2007) and may be able to adapt to new sources of food relatively quickly.

There is not enough known about the relationship between vultures and their food sources. Potential long term consequences of changes to food sources may cause significant changes to Griffon vulture behaviour that are not yet obvious. Of particular interest is the heightened vulnerability of juveniles across all species to human impacts.

Sheep and goats constitute the main food source of griffon vultures. The practice of transhumance livestock management causes the mortality rate to be higher than if all animals were kept confined. This is due to accidents, malnutrition and sickness (Xirouchakis and Mylonas 2005a). Hence, the supply rate of carcasses is higher than for other forms of livestock management. Transhumance is threatened across the Mediterranean due to changes in land ownership practices. Any future changes to livestock management practices may have a large negative impact on the Crete Griffon populations. Although this seems unlikely at this stage, as there has been a large increase in livestock since Greece joined the EU in 1981. A study of the relationship between griffon distribution and the food available is required to understand whether increased food abundance has an implication of higher food availability and what this means for the griffon population in the future (Xirouchakis and Mylonas, 2005).

1.3. Research Objectives

1.3.1. General Objective

The general objectives of this research are to investigate the amount of biomass available as food for Griffon vultures, model the distribution of Griffon vultures, and then to test for any correlation between griffon distribution and available food.

1.3.2. Specific Objectives

- Produce a map of the available food for Griffon Vultures on Crete based on livestock census data and information from livestock owners.
- Model the current food requirements of the Griffon vulture population.
- Generate a foraging distribution model for Griffon Vultures on Crete, based on environmental variables including food availability for summer and winter, adults and juveniles.
- Generate a foraging distribution model for Griffon Vultures on Crete, based on environmental variables excluding food availability for summer and winter, adults and juveniles.

1.4. Research Questions

- What is the food availability on Crete for Griffon Vultures and how is this distributed? What is the food requirement of Griffon Vultures on Crete? Is the food requirement met by the dead biomass distribution?
- Does the location of dumpsites have a significant contribution to the Griffon foraging distribution?
- Is there a significant difference between the foraging distribution for Griffon Vultures in summer and winter?
- Is there a significant difference between the foraging distribution for Griffon Vulture adults and juveniles?
- Is there a significant difference between Griffon Vulture foraging distribution models including food availability and those excluding food availability?

1.5. Research Hypotheses

Hypothesis 1

H₀: That food availability for Griffon Vultures is not significantly higher above 600m altitude.

H₁: That food availability for Griffon Vultures is significantly higher above 600m altitude.

Hypothesis 2

H₀: That dumpsites do not contribute more than 10% to the Griffon Vulture foraging distribution model.

H₂: That dumpsites contribute more than 10% to the Griffon Vulture foraging distribution model.

Hypothesis 3

H₀: There is not a significant difference in the Griffon Vulture foraging distribution between summer and winter.

H₁: There is a significant difference in the Griffon Vulture foraging distribution between summer and winter.

Hypothesis 4

H₀: There is not a significant difference in the Griffon Vulture foraging distribution for adults and juveniles.

H₁: There is a significant difference in the Griffon Vulture foraging distribution for adults and juveniles.

Hypothesis 5

H₀: There is not a significant difference between food included and food excluded Griffon Vulture foraging distribution models.

H₀: There is a significant difference between food included and food excluded Griffon Vulture foraging distribution models.

2. Method

2.1. Research Workflow

There are two stages to this research. The first stage is to determine the food availability for Griffon Vultures and compare this to the requirements of the current Griffon Vulture population. The second stage is to model the foraging of griffon vultures, using species distribution modelling, to determine whether food availability plays a significant role. Details of the method used for food availability is in section 2.3. Details of the method used for species distribution modelling is in section 2.4.

2.2. Study Area

Crete is the largest island belonging to Greece and is located approximately 160km to the south east of the Greek mainland (35°N 24°S)(Figure 1). It has an area of 8336 km² with a length of 260km and variable width between 12 and 60km. The coastline has a length of 1046km. Crete has a very rugged interior and features several high mountain ranges. The highest mountain, Mt. Psiloreitis, has an altitude of 2456 m, followed by Lefka Ori at 2452m. The landscape also features many gorges and cliffs. This distinctive topographical pattern has been shaped by the karst formations which characterise the geology of the area. Between the four main mountainous areas lie relatively flat fertile valleys, with Mesara in the south being the most productive.

Crete has a temperate climate. The temperature at low lying altitudes is mild throughout the year, although the higher peaks experience more extreme weather. This is due to the moderating effect of the surrounding ocean, which also causes high humidity. The island experiences many different micro-climates which, along with the geographic isolation, have contributed to the high biodiversity found in the region. The prevailing wind is from the north and, as the mountain range divides the island in the east west direction, two distinct climates are created.

The wind conditions, steep topography and numerous cliffs make Crete an ideal habitat for vultures. Apart from the Eurasian Griffon Vulture (*Gyps fulvus*), the Bearded Vulture (*Gypaetus barbatus*) is also present.



Figure 1 Map of study area. Greece is shown in the top map, with Crete inside the box, the area inside the box is shown below.

2.3. Food Availability Method

2.3.1. Food Availability Data

2.3.1.1. Livestock Census Data

The livestock census data was obtained from the NHMC, and is a translation of the official census undertaken every 10 years in Greece. The variables used were sheep heads, sheep holdings, goat heads and goat holdings as sheep and goats make up the largest portion of the Griffon diet on Crete (Xirouchakis, 2009). From these variables, a new variable representing the holding size was derived by dividing the total number of sheep and goats in the census collection area by the number of holdings in the area to give an mean holding size within a census collection area.

2.3.1.2. Topographic Variables

The topographic variables used in this part of the research were slope and elevation. The slope(%) was derived for this research from the DEM using the Spatial Analyst toolbar in ArcGIS. These variables were derived from the NASA Shuttle Radar Topographic Mission (SRTM) digital elevation model (DEM) which has been interpolated to 250m by CGIAR-CSI(Jarvis, Reuter, Nelson, & Guevara, 2008). This processing also removed any holes from the original SRTM DEM dataset. The processing method used by CGIAR-CSI is described by Reuter et al. (2007) (Reuter, Nelson, & Jarvis, 2007).

2.3.1.3. Climatic Variables

The climatic variables used in this section of the research were annual precipitation and minimum temperature in the coldest month. These variables were obtained from the WORLDCLIM database (Worldclim, 2009) which is a free data source for mapping and spatial modelling. WORLDCLIM is an online database containing global temperature and precipitation data, as well as derived variables available in a range of spatial resolutions (30 arc-second, 2.5 arc-minutes, 5 arc-minutes and 10 arc-minutes). It is available as historical data incorporating the period 1950 – 2000, and also for future scenarios using data from climate modelling.

For this research, historical data with a spatial resolution of 30 arc-seconds (approx. 1km), was resampled to a resolution of 250m and the missing tile was filled using inverse distance weighting (IDW) interpolation.

2.3.1.4. Land Cover

The land use dataset used was CORINE Land Cover (CLC) 2000, which is produced by the European Environment Agency (EEA). The dataset from 2000 was used as this coincides best with the livestock census. CORINE data delineates the land cover for an area at scale of 1:100000, with the smallest mapping unit being 25 hectares, and assigns a particular class (Commission of the European Communities, 1994). The classes can be found in the appendix (Section 7.2).

2.3.2. Food Availability Analysis Method

2.3.2.1. Flowchart

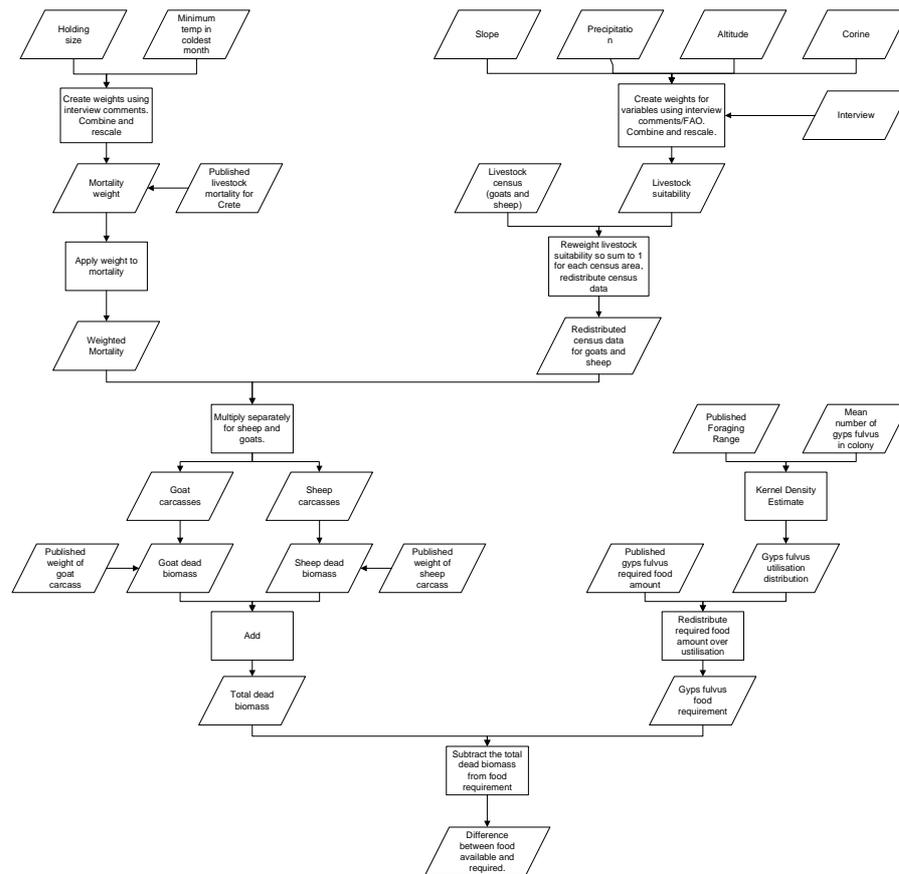


Figure 2 Food Availability Analysis Method Flowchart

The flowchart in Figure 2 above shows the structure of the analysis method used to determine the food availability. The initial steps are to determine the mortality

distribution and to redistribute the livestock census data. The mortality distribution was then applied to the redistributed livestock census data to determine the carcass distribution for sheep and goats, separately and combined. Total dead biomass was calculated using a value published for carcass weights and the number of carcasses. Finally, the dead biomass was compared to the *gyps fulvus* food requirement.

2.3.2.2. **Redistribution of Livestock census data**

A livestock suitability weight was estimated using data on environmental parameters. The environmental parameters used were precipitation, altitude, slope and land cover. This was then applied to the livestock census data to redistribute livestock within census data collection areas to improve the spatial resolution of the census data. The result was livestock redistributed within census collection areas on a 250m grid.

Precipitation was weighted using a linear function to rescale the original values between 497mm and 1066mm to values between 0.5 and 1:

$$W_p = 36.2339782 \times \frac{0.5x}{569.5389709}$$

W_p = precipitation weight

x = precipitation

Elevation was assumed to have a parabolic relationship with livestock suitability on the basis of field observations, and a function was determined so that weight values ranged between 0.5 and 1 for the range of altitude. Three different values of elevation were tested for the maximum weight value of 1, these being 1000, 1500, and 2000. The value of 1500 gave the best representation on visual inspection and this value was implemented using the equation below:

$$W_e = -x^2 + 0.625960868x + 0.5$$

W_e = elevation weight

x = DEM rescaled to between 0 and 1

Slope was reclassified into suitability values determined by the Food and Agriculture Organisation of the United Nations (FAO). These values are given in Table 1.

Table 1 **FAO classification of slope for livestock suitability where 1 is highly suitable and 0 is unsuitable.**

Slope(%)	Suitability Weight
0 - 15	1
15 – 30	0.75
30+	0.25

CORINE land cover was reclassified into suitability according to information collected during interviews with livestock owners, and field observations. The weighting given to each class can be found in the Appendix (Section 7.4).

The sum of the weighting factors for precipitation, elevation, slope and land cover was calculated to determine a relative indicator of the combined effect of the environmental parameters. The result was rescaled to values between 0 and 1.

The weight was then redistributed so that the weight within livestock census collection areas summed to one. This was implemented using zonal statistics. This was so that the total number of livestock collected in the census was maintained.

The relative indicator was then applied separately to the census values for the number of sheep and goats. Only sheep and goats were considered as these are the dominant livestock and make up the bulk of the diet of Griffon Vultures on Crete (Xirouchakis S. , 2005). The result is that the sheep and goats are redistributed within the livestock census collection areas according to the assumed combined effect of the environmental parameters.

2.3.2.3. Mortality Distribution

Mortality distribution was calculated taking into account the factors which were identified by livestock owners as the prevalent causes of mortality. These were freezing, due to low overnight temperatures, and the size of the flock. The size of the flock is an indicator of whether the animals are bound for domestic consumption or are commercial. Flocks of less than 50 animals are generally considered to be destined for the owners table, and hence the utmost care is taken with these animals, including use of preventative medicine. The reason given for this relationship is the expense of medication, as owners with fewer livestock are more likely than the commercial farmers to use the medication. The owners of the commercial flocks do not take the same care with their animals, and hence have a higher mortality rate.

The minimum temperature in the coldest month was used as a proxy for low overnight temperatures and then this was converted into a weighting factor using an exponential function. The exponential function was chosen as it best represents the relationship between temperatures and mortality, given that a change at low temperatures has a much greater impact than a change at higher temperatures.

The equation used to calculate the weighting for min temperature was:

$$w_{mt} = e^{-0.1x}$$

w_{mt} = minimum temperature weight

x = minimum temperature in the coldest month

The value of 0.1 was adopted as an empirical parameter in order to represent, by means of an equation, the relationship which was described during the interviews. The result was then rescaled to a value between 0 and 0.1.

The holding size weighting factor was calculated by combining the number of sheep and goats in the census data and then dividing this by the number of sheep and goat holdings (equation).

$$\text{Holding size} = (\text{sheep heads} + \text{goat heads}) / (\text{sheep holdings} + \text{goat holdings})$$

A flock size of 50 was used as the value at which the weighting should change from negative to positive as this figure was identified, on the basis of the interviews, as the approximate size where the flock changes from domestic to commercial. The livestock owners stop using medication on the flock at approximately this size. A linear equation was used to distribute the weighting between -0.1 and 0.1 with 50 as the x intercept:

$$w_{hs} = 0.002x - 0.1$$

w_{hs} = holding size weight

x = holding size

An assumption was made that, for flock sizes greater than 100, no further effect on mortality is generated and a value of 0.1 was adopted. A conditional function was used to implement this:

$$w_{hs} = \text{con}[x \leq 100, 0.002x - 0.1, 0.1]$$

with the output values ranging between -0.1 – 0.1 for holding sizes between 0 and 100, and a value of 0.1 for all holding sizes over 100.

These two weighting factors were then combined through addition and divided by a factor of 10 to produce a representative relative weighting map with values ranging between -0.01 and 0.02.

This was then added to a base value of 4% mortality rate published in a study on farming practices in Crete (Stefanakis, Volanis, Zoiopoulos, & Hadjigeorgiou, 2007) to obtain values between 0.03 and 0.06 for mortality. This produces a relative mortality distribution which incorporates models relating mortality rates to minimum temperature and flock size data. The resulting mortality distribution is generally consistent with anecdotal evidence from interviews on the effects of flock size and minimum temperature. With regard to the range of values produced by the above distribution process, these are also consistent with anecdotal evidence from interviews, except that some livestock owners with small flocks at low altitudes reported nil losses, and some livestock owners with larger flocks at high altitudes reported losses of up to 15%.

2.3.2.4. Carcass Distribution

The estimated carcass distribution was determined by applying the mortality distribution to the redistributed livestock census data. This was done separately for sheep and goats. The result is a number of carcasses per 250m cell for sheep and for goats. This was summed to produce an estimate of the total number of carcasses per cell. This calculation infers that carcass distribution is a direct reflection of livestock distribution. However, this is an approximation as, in practice, many carcasses are either buried or collected together in dumpsites. This may have an influence on the carcass distribution.

2.3.2.5. Dead Biomass

Dead biomass was calculated by multiplying the carcass distribution by a carcass body weight. The carcass body weight used to estimate biomass was selected from another study of biomass available for vultures, so that comparison between locations is possible. The values for standard body weight which were used are 55kg for sheep and 65kg for goats ((Ministerio de Agricultura, Pesca y Alimentacion (1989-1990), 1990-1998) in (Parra & Telleria, 2004). Sheep and goat dead biomass

distributions were calculated separately and then combined to obtain an estimate of total dead biomass.

2.3.2.6. Food requirement

A published value for the food requirement of *gyps fulvus* of 0.45kg per day, or 164.25kg per adult vulture per year (van Beest, van Den Bremer, De Boer, Heitkonig, & Monteiro, 2008), was used to calculate the total food requirement for the Griffon Vulture population on Crete. This was distributed over a griffon utilisation surface to obtain the food requirement for the *gyps fulvus* population on Crete. All vultures were assumed to require the total adult amount, and the population estimate used was the high value of 417 for the published estimated population range on Crete (Xirouchakis & Mylonas, 2005). This value is still current (per. Communication Xirouchakis).

A kernel density function was applied to the colony location data to determine a *gyps fulvus* utilisation surface. This was weighted using the mean number of griffons occupying identified colonies as the weighting factor, and the published foraging range of 14.9km (Xirouchakis, 2009) as the smoothing parameter. This was implemented using Hawth's tools in ArcGIS.

2.3.2.7. Difference between Food Availability and Requirement

The total dead biomass distribution was subtracted from the food requirement distribution to investigate the difference between the food requirement and availability.

2.4. Species Distribution Modelling

2.4.1. Flowchart

2.4.2. *Gyps fulvus* Data

There are two separate forms of data for Griffon Vultures (*Gyps fulvus*) on Crete, one consists of telemetry data and the other of colony locations.

2.4.2.1. Telemetry Data

The Natural History Museum of Crete (NHMC) has collected telemetry data on a number of Griffon vultures over the course of the last decade as part of ongoing research. The telemetry data consists of 1142 points which represent sightings of 15 griffons collected over a period of 6 years from 2003 to 2009. This has been separated into summer and winter, adult and juvenile datasets. The summer and

winter delineation was assumed to be summer April – September, and winter October – March for this research based on interviews conducted with livestock owners regarding when they move their livestock either inside shelter or to another location. Also taken into consideration was a study regarding the average number of griffons in a lowland and highland colony over the course of a year (Xirouchakis, 2005). This was taken into consideration as the griffons have a tendency towards the highland colony in summer and these observations confirmed the dates determined from the interviews. These periods coincide with the observed midpoint of the maximum and minimum seasonal colony populations (Xirouchakis, 2005).

2.4.2.2. Colony Data

The colony data was provided by the NHMC as XY locations with a unique identifier. This was then matched to published material on the mean number of griffons and number of breeding pairs inhabiting each colony over a period of 8 years, from 1995 to 2002 (Xirouchakis & Mylonas, 2005), using the unique identifier, on the assumption that the published results still accurately depict the current situation (per. comm. Xirouchakis).

2.4.3. Predictor variables

Environmental variables have a limiting effect on species distribution (Gusian & Thuiller, 2005). Expert knowledge and field observations were the basis for selection of the environmental variables used in this study.

All data preparation and processing was implemented in ArcGIS. The data layers were all transformed into the WGS84 UTM Zone 35 projection and resampled to a spatial resolution of 250m. All variables subsequently used in Maxent were exported into ASCII format for use with this program.

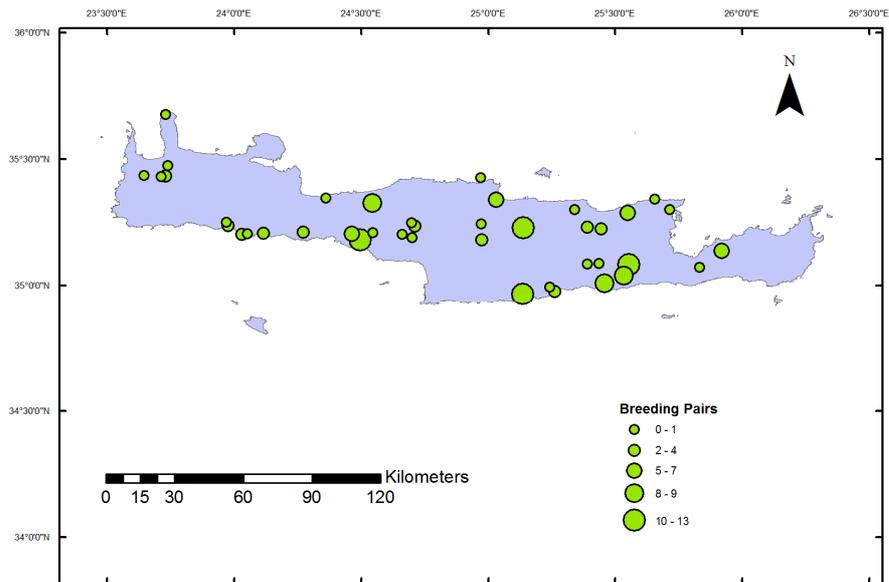


Figure 3. Mean number of breeding pairs in each of the 34 active colonies between 1995 – 2002.

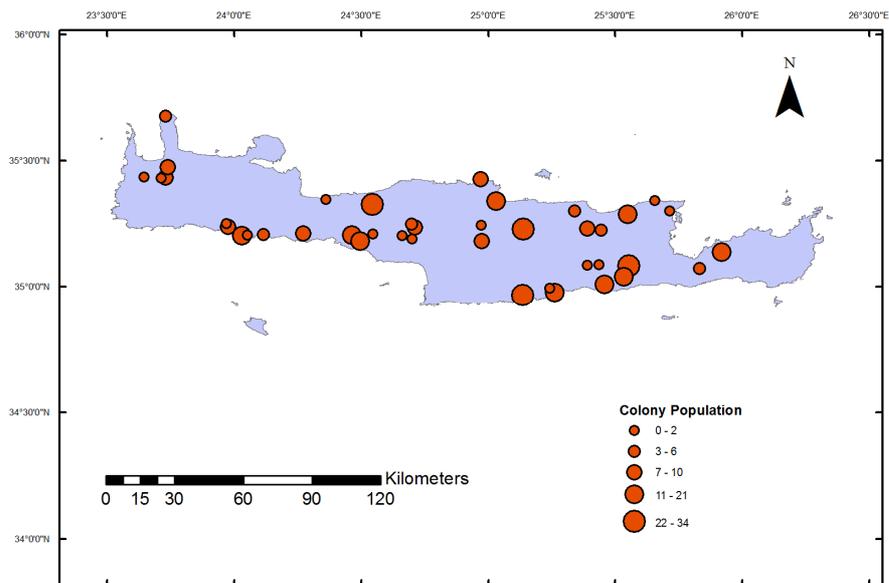


Figure 4 Mean population in each of the 34 active colonies between 1995 – 2002.

2.4.3.1. Climatic Variables

Climatic variables were obtained from the WORLDCLIM database (Worldclim, 2009) which is a free data source for mapping and spatial modelling. WORLDCLIM is an online database containing global temperature and precipitation data, as well as 19 derived variables (BIOCLIM) available in a range of spatial resolutions (30 arc-second, 2.5 arc-minutes, 5 arc-minutes and 10 arc-minutes). It is available as historical data incorporating the period 1950 – 2000, and also for future scenarios using data from climate modelling.

For this research, historical data, with a spatial resolution of 30 arc-seconds (approx. 1km), was resampled to a resolution of 250m and the missing tile was filled using inverse distance weighting (IDW) interpolation.

The variables used in the modelling process are identified in the section on multicollinearity (section 2.4.4.1).

2.4.3.2. Topographic Variables

Topographic variables were derived from the NASA Shuttle Radar Topographic Mission (SRTM) digital elevation model (DEM) which has been interpolated to 250m by CGIAR-CSI (Jarvis, Reuter, Nelson, & Guevara, 2008). This processing also removed any holes from the original SRTM DEM dataset. The processing method used by CGIAR-CSI is described by Reuter et al (2007) (Reuter, Nelson, & Jarvis, 2007). The slope (%) and aspect were derived for this research from the DEM using the Spatial Analyst toolbar in ArcGIS.

Aspect was transformed into separate Southness and Westness variables to highlight the differences between the orientations. The most commonly used method for this involves transforming aspect using sin and cosine functions producing an output which ranges between 1 and -1 (Wallace & Gass, 2008). This method was not producing reasonable results so an alternative set of conditional functions was implemented. These conditional functions are included below:

Southness

$$\begin{aligned} [\text{asp1}] &= \text{Con}([\text{asp}] .180, 360 - [\text{asp}], [\text{asp}]) \\ \text{Southness} &= \text{Con}([\text{asp1}] \geq 0, [\text{asp}], 90) \end{aligned}$$

Westness

[asp2] = Con ([asp] ≥ 0 AND [asp] ≤ 90, 90 – [asp], [asp])
[asp3] = Con ([asp2] > 90 AND [asp2] ≤ 270, [asp2] – 90, [asp2])
[asp4] = Con ([asp3] > 270, 450 – [asp3], [asp3])
Westness = Con ([asp4] ≥ 0, [asp4], 90)

The last line in both series of functions is to eliminate the -1 which is assigned to flat areas.

2.4.3.3. Proximity Variables

Shapefiles of the rivers, towns, dumpsites and roads and locations of the feeding stations were obtained from the NHMC in the Greek Grid projection. These were reprojected into WGS_1984 using the standard transformation available in ArcGIS. Euclidean distance to rivers and the coast were calculated using the Euclidean Distance function in the Spatial Analyst toolbox in ArcGIS.

Euclidean distance to *gyps fulvus* colonies and the feeding location was also calculated in the same manner.

2.4.3.4. Land Cover

The land use dataset used was CORINE Land Cover (CLC) 2000, which is produced by the European Environment Agency (EEA). The dataset from 2000 was used as this coincides best with the livestock census. CORINE data delineates the land cover for an area at scale of 1:100000, with the smallest mapping unit being 25 hectares, and assigns a particular class (Commission of the European Communities, 1994).

2.4.3.5. Dead Biomass

The total dead biomass calculated in the section on food availability (section 2.3.2.5) was used as an input variable for the species distribution modelling.

2.4.4. Species Distribution Modelling Method

2.4.4.1. Multicollinearity

Multicollinearity refers to the correlation between predictor variables (Dohoo et al. 1996, Kovacs et al. 2005). When the predictor variables are more significantly correlated with each other than in comparison to the response variable, it becomes a problem to separate the effects of the predictor variables (Aguilera et al, 2006). Multicollinearity can be detected using pair-wise comparisons. However, this method does not always detect existing linear dependencies (Mansfield & Helms,

1982). A preferred method for checking multicollinearity is the calculation of the Variance Inflation Factor (VIF) shown below:

$$VIF = \sqrt{1 - R^2}$$

Where R^2 is the coefficient of determination.

The VIF represents the inflation in the variance for each regression coefficient compared with a situation of orthogonality. The threshold at which the VIF becomes too large is arbitrary. However, a generally accepted value for eliminating variables is a VIF of 10 (Giacomelli et al. 1998).

Multicollinearity was calculated for the environmental variables using the collinearity diagnostics in SPSS statistical software, with categorical variables excluded as they cannot be tested. The test was run while excluding the variable with the highest VIF at each iteration until all variables had a VIF less than 10. The variables were excluded one at a time as the exclusion may influence the remaining variables.

The aim of removing variables is to maximise the information remaining in the predictor variables and ideally as many variables as possible are retained. Indeed, occasionally it is useful to keep parameters which have a high VIF value if their merit is determined through expert knowledge.

The spatial correlation was not tested as, in species distribution modelling, the potential distribution does not show spatial autocorrelation (Phillips, Dudlik, & Schapire, A Maximum Entropy Approach to Species Distribution, 2004).

2.4.4.2. MaxEnt

There have been many methods proposed for modelling species distributions. These include Generalised Linear Model (GLM) (Peace & Ferrier, 2000, Guisan & Zimmerman, 2000, Beck et al. 2005, Guisan et al., 2002); GARP (Stockwell & Peterson, 1999, Sweeney et al, 2007), ENFA (Chefaoui et al. 2005; Santos et al., 2006, Martinez et al., 2006) and MaxEnt (Phillips et al. 2004, Phillips et al. 2006).

MaxEnt was used in this research as it has been shown to have superior performance when using presence only data as compared to the other available methods (Sergio et al., 2007, Phillips et al, 2006) (Phillips, Dudlik, & Schapire, A Maximum Entropy Approach to Species Distribution, 2004), and also creates outputs which allow

improved interpretation of the key contributing factors of the model (Phillips, Dudlik, & Schapire, A Maximum Entropy Approach to Species Distribution, 2004).

Maximum Entropy (MaxEnt) is a powerful machine – learning method which is applicable in a wide range of fields. It is often used and has recently found favour in the species modelling community. MaxEnt has a precise mathematical formulation which ensures that the maximum entropy of the event is identified. Specifically, MaxEnt takes a set of samples and a set of features and estimates the distribution by finding the empirical average of the features across the samples(Phillips, Dudlik, & Schapire, A Maximum Entropy Approach to Species Distribution, 2004). The algorithm used in MaxEnt is an iterative approach to sequentially determine the weights on the features. This allows very large feature spaces to be investigated (Phillips, Dudlik, & Schapire, A Maximum Entropy Approach to Species Distribution, 2004). The model is based on the maximum entropy principle which states that the best available predicted distribution is one which maximises the input information entropy and the output is the niche the species occupies (Phillips, Dudlik, & Schapire, A Maximum Entropy Approach to Species Distribution, 2004). Usually, the input data is a range of environmental variables and the niche is defined in terms of these environmental variables (Phillips, Dudlik, & Schapire, A Maximum Entropy Approach to Species Distribution, 2004). The potential distribution is then defined in terms of the environmental variables which correspond to the species occurrence data(Anderson, Lew, & Peterson, 2003).

The MaxEnt method for species distribution initially determines the distribution of the predictor variables in the available presence cells, and then a probability condition which satisfies the variable distribution as uniformly as possible is chosen (Buehler & Ungar, 2001). This results in pixels with a similar distribution of predictor variables to the training data receiving a high probability, and pixels with a very different distribution receiving a low probability.

MaxEnt was used in this study of griffon vultures to determine which parameters drawn from environmental, topographic and anthropogenic variables correlated the most with the foraging and nesting distribution. In this research the presence data consists of two types, telemetry data and colony locations. The telemetry data is assumed to be foraging locations, whereas the colony locations are considered to be nesting sites.

The spatial resolution of all variables was 250m and all variables used were continuous, except land cover (CORINE) and geology. The model was run using

70% of the points for training, with 30% used for the accuracy assessment. Models were run with 100 repetitions using a random seed for the starting point.

2.4.5. Statistical Analysis

Model evaluation is an important part of any modelling process. The receiver operating characteristics (ROC) method is used for assessing the accuracy of the model with 70% of the data used for training and the remaining 30% of the data kept as testing data for assessing the accuracy of the model. MaxEnt uses the jack-knife method with bootstrapping to assess the importance of the input parameters. This involves running the model, taking out each variable in sequence and assessing the output without that variable. MaxEnt also runs the model for the scenario where only a single variable is included.

2.4.5.1. Receiver Operating Characteristics (ROC) Curves

A method of evaluating the quality of the model involves looking at Receiver Operating Characteristics (ROC) curves. These are a graphical representation of the proportion of false positive and false negatives for every threshold (Fielding and Bell, 1997) (Phillips, Dudlik, & Schapire, A Maximum Entropy Approach to Species Distribution, 2004). False negatives and false positives are usually determined by cross-tabulation of data in a confusion matrix. However, this requires both presence and absence data. Alternatively however, when absence data is not available, it is still possible to assess the model against a random model. In this case, all pixels are assigned an absence value on the basis that this is random ((Phillips, Dudlik, & Schapire, A Maximum Entropy Approach to Species Distribution, 2004) Phillips et al. 2006).

The area under the curve (AUC) can be interpreted statistically as the probability that the model will correctly discriminate between the positive and negative values from a randomly chosen pair. Theoretically, the highest value possible is 1, indicating that the model will always distinguish the positive and negative values. However, as only presence and pseudo-absence (random) data is used in MaxEnt, the maximum AUC is less than 1 (Phillips, Dudlik, & Schapire, A Maximum Entropy Approach to Species Distribution, 2004) and 0.5 indicates the model is no better than random.

Analysis of MaxEnt models is facilitated by the inclusion of the area under the curve (AUC) in the model outputs. This is a statistical measure of the value under the receiver operating characteristic (ROC) curves (Phillips, Dudlik, & Schapire, A Maximum Entropy Approach to Species Distribution, 2004). The AUC is calculated

for each run and this makes comparison between runs possible. The averaged value for multiple runs gives an estimate of the accuracy of the model.

The distributions were tested with the Wilcoxon's Match Pairs test, which is a nonparametric equivalent of the t-test and does not assume normal distribution of the data. For more information see (Siegel & Castellan, 1988).

2.5. Employed Software

The spatial information processing was handled in ESRI ArcGIS 9.3 and the species distribution modelling was performed using MaxEnt 3.3.1. The collinearity diagnostics was performed in SPSS 16.0. Nonparametric statistics were performed in Statistica 7.0.

3. Results

This chapter discusses the main findings of the research. These are divided into two main sections. The first is food availability for griffon vultures on Crete, and the second is distribution modelling to investigate the impact of food availability.

Interviews were conducted with local livestock owners to facilitate a better understanding of the environment that the griffon vultures on Crete inhabit. While it was anticipated that it would be possible during these interviews to collect quantitative data on the livestock density, this proved to be incorrect. Due to the difficulties arising from the general reticence of the farmers, the language translation interpretation and the informal circumstances of the interviews, the only quantitative data which could be collected was a mortality estimate for each interview location.

Information was difficult to obtain from livestock owners through interviews. Livestock owners were suspicious, defensive and extremely unwilling to reveal numbers, particularly to foreign students from a Dutch university.

3.1. Food Availability

As described in section 2.3, food availability was determined for griffon vultures with intermediate results for the total number of carcasses and the total dead biomass. The initial stage distributed a mortality rate over Crete (Figure 5). This shows a distinct pattern with higher mortality in the mountainous areas and lower mortality in the lower lying valleys.

Without further input or reference to other information, Figure 5 would lead to a conclusion that the areas in central Crete are likely to yield the highest level of available food. Such a conclusion would then be supported by a significantly higher density of livestock in these areas. The livestock suitability weight shows some indication of this apparent pattern with a high suitability weighting for the central Crete area (Figure 6). When this is redistributed and applied to the census data, a marked pattern is apparent, with very high numbers of livestock in the cells in the central Crete areas for both the goats and sheep. This is also apparent in the combined redistributed livestock (Figure 7).

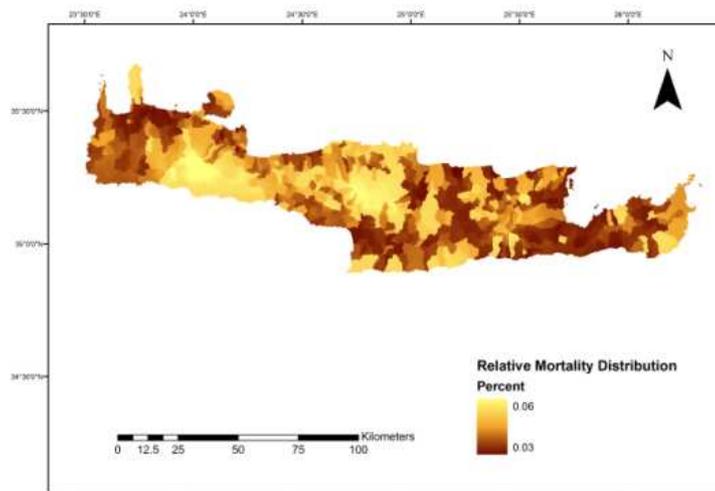


Figure 5 Mortality rate which was increased or decreased according to the information from the interviews to represent the spatial pattern of mortality on Crete.

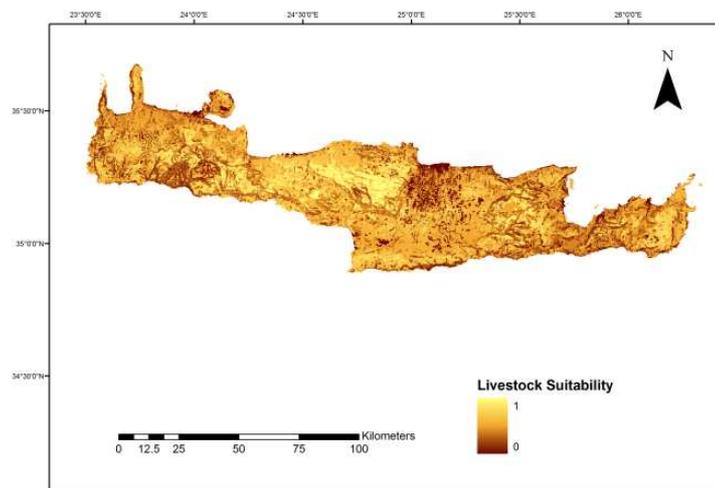


Figure 6 Livestock Suitability Weighting map based on environmental variables used to redistribute livestock census data within census collection polygons.

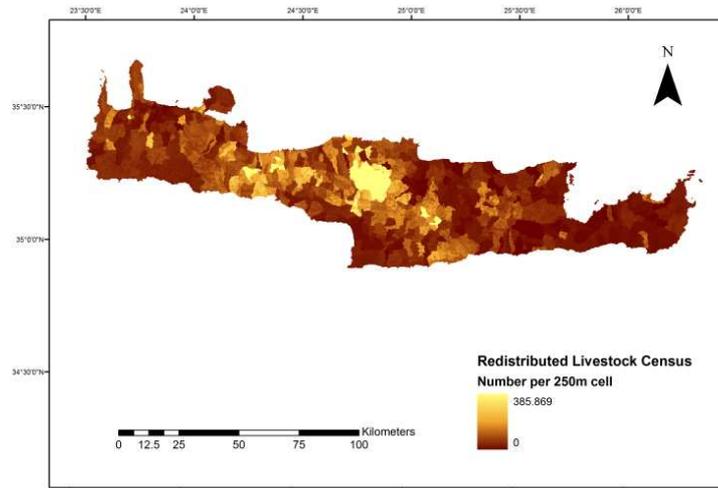


Figure 7 Livestock Census redistributed on the basis of environmental variable within the census collection polygons.

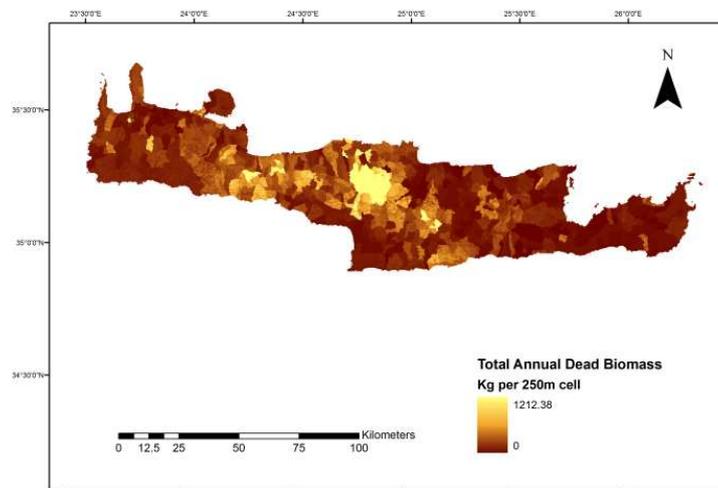


Figure 8 The combined annual dead biomass from sheep and goats available as food for Griffon Vultures.

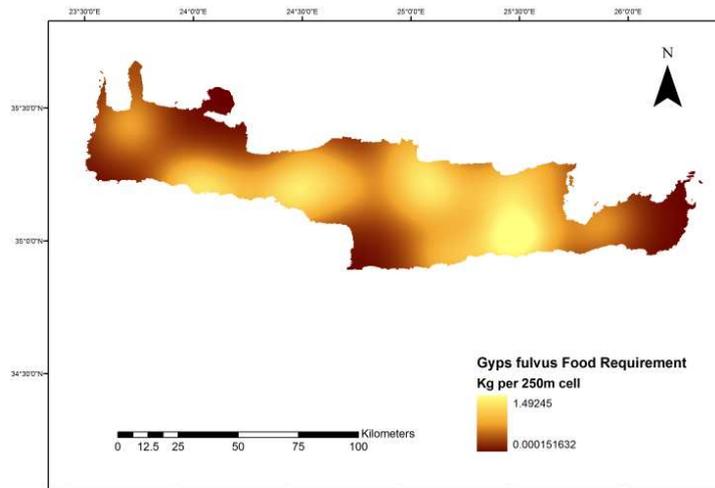


Figure 9 *Gyps fulvus* Food Requirement based on a calculated requirement of approximately 70 000kg per annum distributed over a kernel density function using the colony locations as points, mean number of Griffon vultures inhabiting colony as weighting factor and foraging range as smoothing parameter.

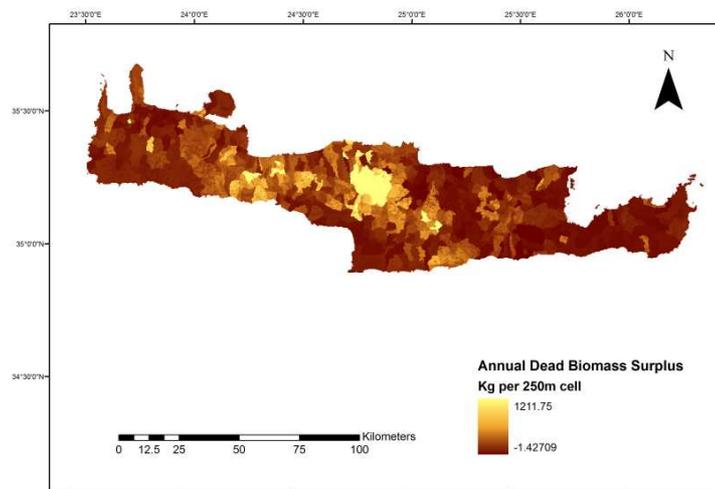


Figure 10 Annual Dead Biomass Surplus. The combined sheep and goat dead biomass with the *gyps fulvus* food requirement deducted.

The carcass numbers per cell clearly show a marked concentration in the central mountainous area of Crete for both goat and sheep. The number for sheep is generally much higher than for goats, with the maximum number of sheep carcasses being approximately 15, whereas the number of goat carcasses has a maximum of approximately 7. These areas coincide and the overall maximum is 20 carcasses concentrated in the central mountainous area.

The food requirement to sustain the maximum current population is remarkably low when distributed over Crete according to the utilisation distribution (Figure 9), with a maximum value of 1.49kg per 250m cell and an overall requirement of approximately 70 000kg distributed over Crete. The available food in the form of combined biomass from sheep and goats has cell values of up to 1212kg, which is an order of magnitude larger. This creates an overall food surplus (Figure 10).

3.2. Species Distribution Modelling

3.2.1. Multicollinearity

Collinearity is a problem as it interferes with the model and may cause over-fitting to the training data. However, on Crete almost all of the environmental predictor variables have high levels of apparent collinearity. Despite the high levels of collinearity, VIF values of less than the commonly used threshold of 10 were achieved with 17 continuous variables. The two categorical variables, land cover and geology, could not be tested using the linear regression method. The variables included in the model are listed below, along with the VIF values, in Table 2.

Table 2 VIF values for the predictor variables included in Maxent Modelling

Predictor Variable	VIF
Actual Evapotranspiration	1.540
Annual Mean Temperature	9.581
Annual Precipitation	7.727
Total Dead Biomass	1.317
Cloud Cover	8.314
Colony Distance	1.251
Altitude	9.165
Dumpsite Distance	1.622
Feeding Location Distance	1.891
Irradiation	9.268
Mean Diurnal Range	8.132
MODIS NDVI	2.103
Distance to roads	2.128
Slope	1.220
Southness	1.224
Town Distance	2.641
Westness	1.170

3.2.2. Model Results

Using the presence data obtained from telemetry and described in section 2.4.2.1, the Maximum Entropy Model was utilised to generate foraging distribution models. The MaxEnt model creates a probability distribution based on the maximum entropy. This model was run including the dead biomass distribution and then excluding dead biomass distribution and the results were compared using nonparametric statistics. By running a species distribution model in MaxEnt using different combinations of variables, eight different scenarios have been investigated. These were the various combinations of adult and juvenile, and summer and winter identified in Table 3.

Table 3 Scenarios run in MaxEnt species distribution modelling.

	<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>6</i>	<i>7</i>	<i>8</i>
Adult	•	•			•	•		
Juvenile			•	•			•	•
Summer	•		•		•		•	
Winter		•		•		•		•
Food Inclusive	•	•	•	•				
Food Exclusive					•	•	•	•

The model was run using these scenarios to test whether the abundance of available food had a significant effect on the *gyps fulvus* foraging distribution. From the large surplus determined in the food availability section, it could be assumed that the food abundance is such that this is not a determining factor in the foraging distribution models. Indeed, this was the case, with no discernable difference between the models run with the dead biomass included, and those run without. This can be seen from the ROC analysis which shows that there is no difference in the area under the curve (AUC) value for 100 bootstrap repetitions of the models run either with or without dead biomass.

Table 4 AUC analysis for MaxEnt models with and without inclusion of dead biomass.

	Test AUC (including dead biomass)	Test AUC (excluding dead biomass)
Adult Summer	0.9542	0.9779
Adult Winter	0.9669	0.9882
Juvenile Summer	0.9582	0.9794
Juvenile Winter	0.9464	0.9785

The AUC for all models is very high, as all are above 0.95 which is very close to the theoretical maximum value of 1. This indicates excellent models which performed much better than random prediction. The maps of the distribution for the models () appear consistent with the conditions which were observed in the field and overall the model appears to predict the foraging distribution of *gyps fulvus* very well.

The modelled foraging distribution results show high probability values through the central section of Crete, corresponding to the arid mountainous regions. These are also the regions which show high livestock census values and following from this high food availability. See Figures 11 – 18 for foraging distributions of Griffon vultures under various scenarios.

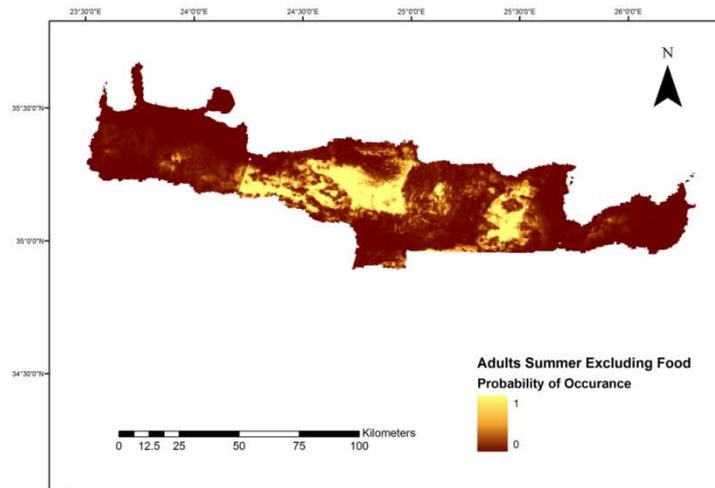


Figure 11 Griffon foraging distribution for adults in summer excluding food availability modelled using Maxent. Values range from 0 to 1 representing probability of occurrence.

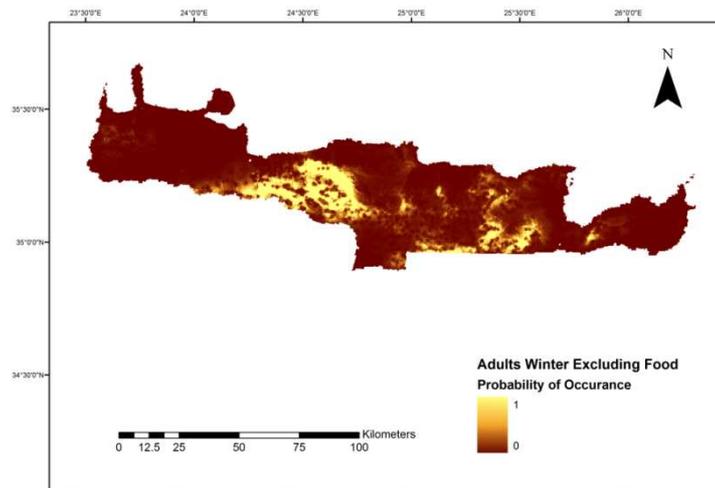


Figure 12 Griffon foraging distribution for adults in winter excluding food availability modelled using Maxent. Values range from 0 to 1 representing probability of occurrence.

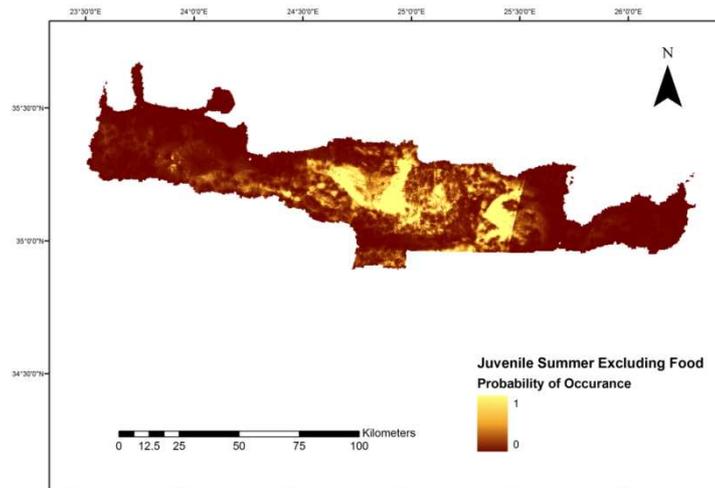


Figure 13 Griffon foraging distribution for juveniles in summer excluding food availability modelled using Maxent. Values range from 0 to 1 representing probability of occurrence.

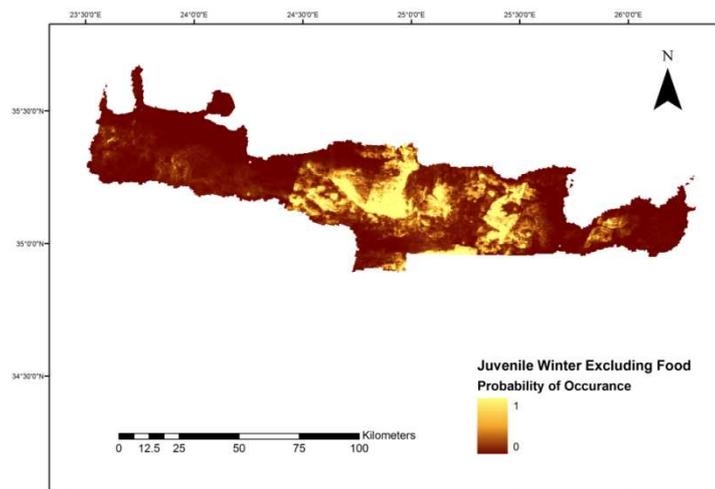


Figure 14 Griffon foraging distribution for juveniles in summer excluding food availability modelled using Maxent. Values range from 0 to 1 representing probability of occurrence.

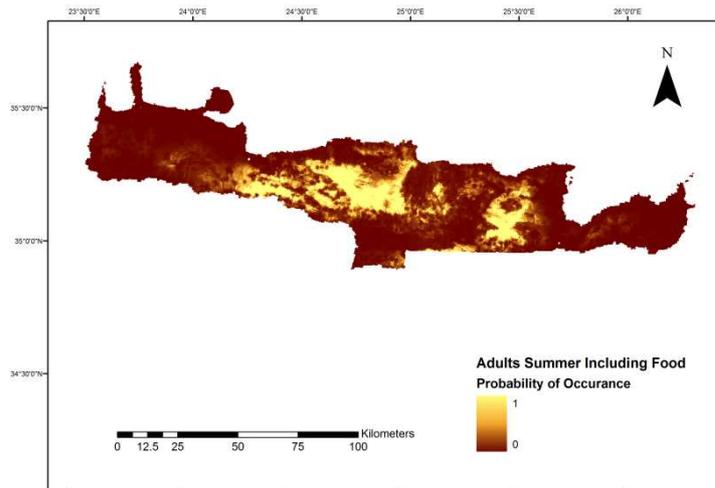


Figure 15 Griffon foraging distribution for adults in summer including food availability modelled using Maxent. Values range from 0 to 1 representing probability of occurrence.

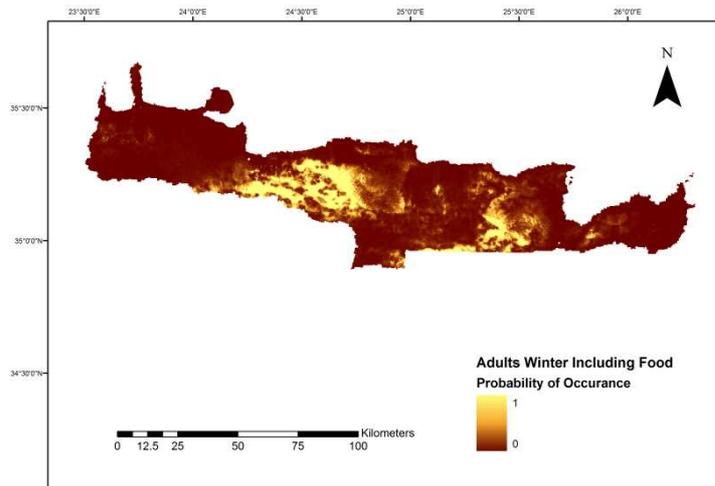


Figure 16 Griffon foraging distribution for adults in winter including food availability modelled using Maxent. Values range from 0 to 1 representing probability of occurrence.

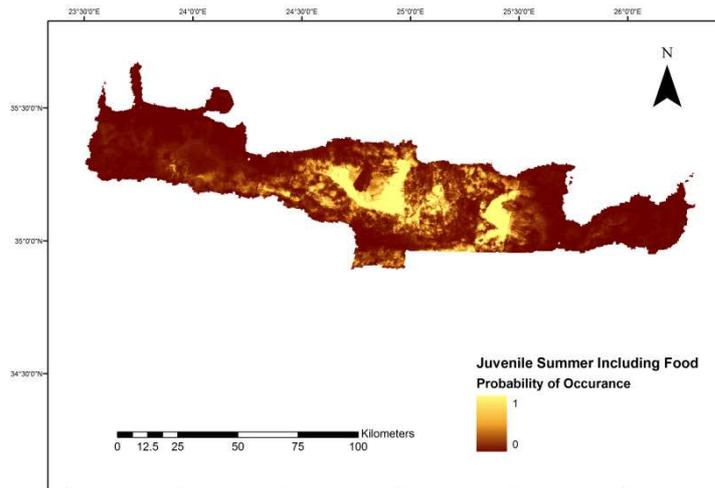


Figure 17 Griffon foraging distribution for juveniles in summer including food availability modelled using Maxent. Values range from 0 to 1 representing probability of occurrence.

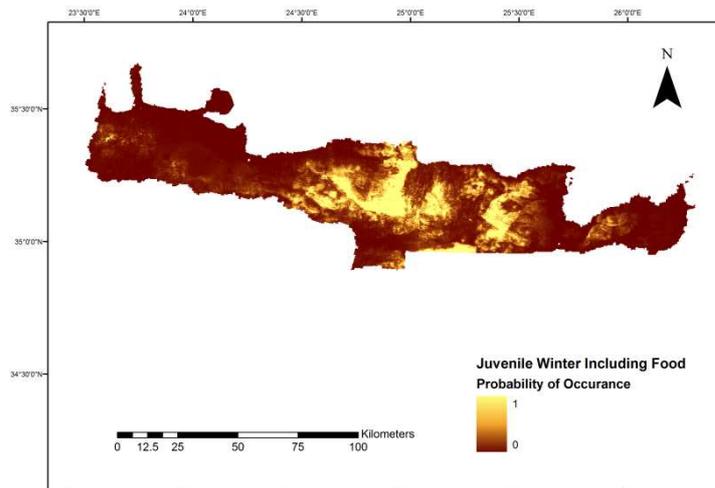


Figure 18 Griffon foraging distribution for juveniles in winter including food availability modelled using Maxent. Values range from 0 to 1 representing probability of occurrence.

3.2.3. Importance of the predictor variables

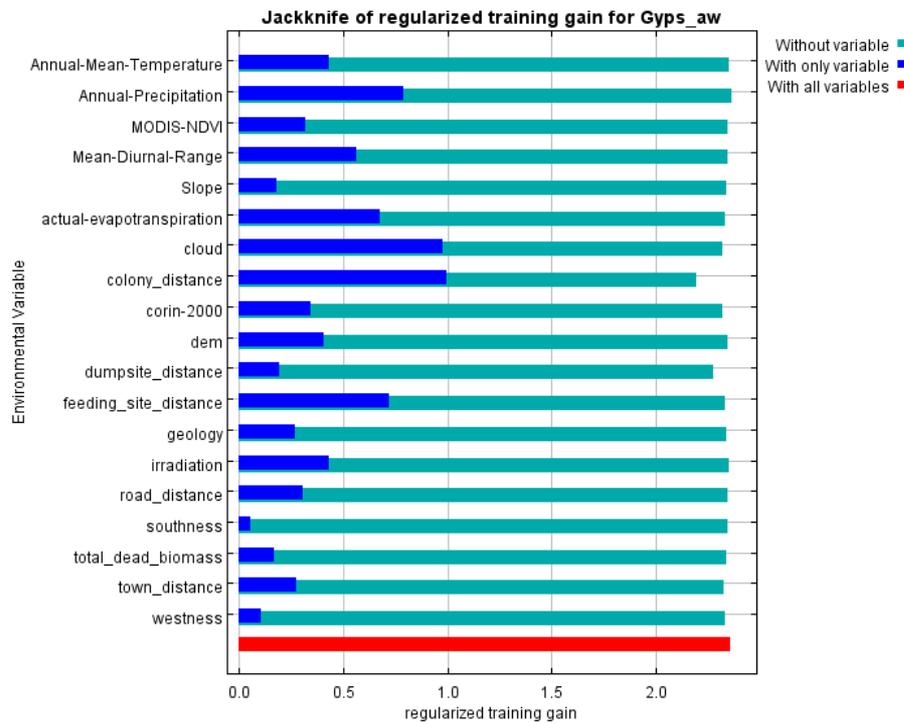


Figure 19 Jackknife of regularized training gain for the Adult Winter food inclusive model.

The most important variables across all models in the jackknife method were the cloud cover, colony distance and annual precipitation. These variables had the highest gains in isolation across all scenarios, and also most decreased the gain when omitted. In Figure 16 the jackknife test for the adult winter food included scenario shows that, for this model, the colony distance had both the highest gain in isolation, and also most decreased the gain when omitted, indicating that this is the most important variable for this model.

Distance from colony correlation shows a clear relationship to probability of occurrence, and beyond 15km there is an extremely low probability of presence. This corresponds to the published foraging range (Xirouchakis 2009) which was used to determine the *gyps fulvus* utilisation function in section 2.3.2.6.

The three variables which have the highest influence across all models are the annual precipitation, cloud cover and the distance to colonies (Appendix 7.1). Generally, areas with a higher precipitation also have a higher probability of occurrence. A representative graph of this relationship is shown in Figure 20. The relationship shows a maximum slightly above 1000mm precipitation, which is also shown in the other 7 model scenarios. However, the adult winter and all juvenile models show a more pronounced drop off after the maximum. This indicates that there may be a threshold beyond which *gyps fulvus* are less likely to occur as it is too wet.

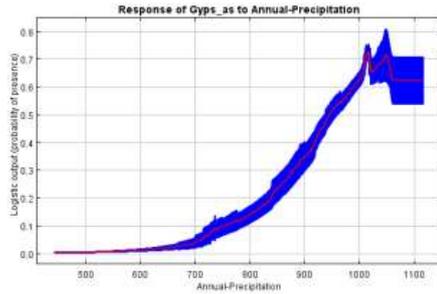


Figure 20 Response curve for 100 repetitions of annual precipitation for the Maxent model run for adults in summer excluding dead biomass.

The cloud cover response curves generally show a pronounced peak in the low values of cloud cover and a second peak in the higher values, although there are differences between the different scenarios. An example of the cloud response curve is Figure 21.

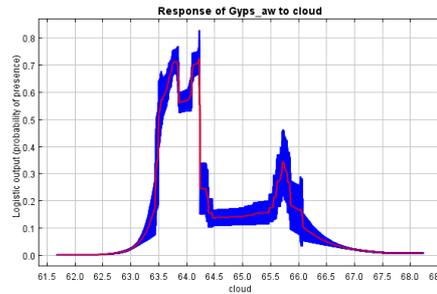


Figure 21 Cloud response curve for adults in winter excluding dead biomass.

The response curves for cloud cover are quite different for the different model scenarios, although the difference between with and without dead biomass is negligible. This is an unexpected result given that there is no difference in the input cloud data, which is an average for the year. This is of interest as cloud cover is reported to be contributing to the model by between 9.5 to 30.5%. Although the cloud cover values apparently differ between the summer and winter presence points, this difference may not actually reflect the environmental conditions as seasonality in cloud cover is not represented in the input data.

The third variable which has a significant contribution to the models is the distance to the colonies. The results are similar for all modelling scenarios and show exponential decay with distance. The probability reaches close to zero at approximately 15km from the colony which confirms the mean foraging distance used in the kernel density estimate for distributing the food requirement (Xirouchakis & Andreou, Foraging behavior and flight characteristics of Eurasian griffons *Gyps fulvus* in the island of Crete, Greece, 2009). A representative example can be seen in Figure 22.

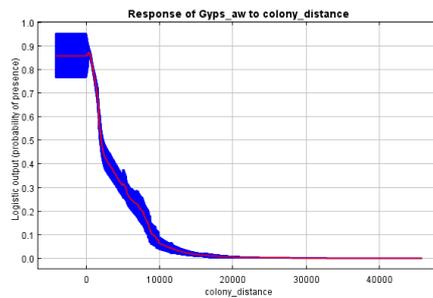


Figure 22 Colony distance response curve for adults in winter excluding dead biomass.

It is clear from the response curves that there is a distinct difference in foraging distribution patterns between adults and juveniles relative to dumpsite location. Juvenile Griffons appear to forage within 5km of dumpsites, whereas adults range over a wider territory. This may indicate that juveniles are more reliant on finding food in these locations, as compared to the more experienced adults. However, the distance to dumpsites contributes a maximum of 3.2% so the null hypothesis can be accepted for Hypothesis 2.

Aspect did not contribute more than 3% to the model which is surprising as when presence records are overlaid on aspect an inclination towards southern facing slopes appears to be visible.

3.2.4. Statistical Analysis

A Wilcoxon Matched Pairs test was performed to test for significant difference between the scenarios implemented in Maxent.

Testing the hypothesis that there is a significant difference at the $p < 0.05$ level in Griffon Vulture distribution between summer and winter shows that there is a significant difference between the Griffon foraging distributions in summer and winter for the food excluded adult models, and for both juvenile models (Table 5). The adult food included models do not show a significant difference between summer and winter. It can be concluded that there is a significant difference in Griffon foraging distributions between summer and winter.

Table 5 Results for the Wilcoxon Matched Pairs test for comparing the Maxent average logistic prediction results over 100 replicated bootstrap runs. The pairs are separated into summer and winter models. The values in bold are statistically significant at $p < 0.05$.

Model Scenario 1	Model Scenario 2	z	p-value
Adult Summer Food Inclusive	Adult Winter Food Inclusive	1.181	0.238
Adult Summer Food Exclusive	Adult Winter Food Exclusive	2.503	0.012
Juvenile Summer Food Inclusive	Juvenile Winter Food Inclusive	6.812	0.0000000001
Juvenile Summer Food Exclusive	Juvenile Winter Food Exclusive	3.232	0.001

Testing the hypothesis that there is a significant difference in Griffon Vulture distribution between adults and juveniles shows that there is a significant difference between the foraging distributions only in winter when food is included (Table 6). It can be concluded that there is not a significant difference in Griffon foraging distributions between adults and juveniles in summer. The models showing a significant difference is between adults and juveniles in winter with food included

may indicate that adults and juveniles display different foraging behaviour during this season.

Table 6 Results for the Wilcoxon Matched Pairs test for comparing the Maxent average logistic prediction results over 100 replicated bootstrap runs. The pairs are separated into adult and juvenile models. The values in bold are statistically significant at $p < 0.05$.

Model Scenario 1	Model Scenario 2	z	p-value
Adult Summer Food Inclusive	Juvenile Summer Food Inclusive	1.177	0.239
Adult Summer Food Exclusive	Juvenile Summer Food Exclusive	0.068	0.945
Adult Winter Food Inclusive	Juvenile Winter Food Inclusive	5.251	0.000002
Adult Winter Food Exclusive	Juvenile Winter Food Exclusive	1.129	0.259

Testing the hypothesis that there is a significant difference in Griffon Vulture distribution between food included and food excluded models shows that there is a significant difference between the foraging distributions for all pairings except adults in winter (Table 7). This supports the above results for the difference in adults and juveniles by showing that, in winter, adults and juveniles display different behaviour as, for juveniles, the food inclusion in the model is significant whereas, for adults in winter, it is not significant.

Table 7 Results for the Wilcoxon Matched Pairs test for comparing the Maxent average logistic prediction results over 100 replicated bootstrap runs. The pairs represent food included and food excluded models. The values in bold are statistically significant at $p < 0.05$.

Model Scenario 1	Model Scenario 2	z	p-value
Adult Summer Food Inclusive	Adult Summer Food Exclusive	10.652	0.000
Adult Winter Food Inclusive	Adult Winter Food Exclusive	1.877	0.061
Juvenile Summer Food Inclusive	Juvenile Summer Food Exclusive	10.606	0.000
Juvenile Winter	Juvenile Winter	12.111	0.000

Food Inclusive	Food Exclusive		
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In summary, food availability is significantly greater above 600m, however the food availability does not contribute more than 10% to the Griffon Vulture foraging distribution models. There is a significant difference in the Griffon Vulture foraging distance in summer versus the foraging distribution in winter. There not a significant difference between the foraging distributions of adults and juveniles. Finally, food availability is significant in modelling Griffon foraging distributions. The environmental variables which contributed the most to the models were cloud cover, annual precipitation and the distance to colonies.

4. Discussion

Food availability is generally considered to be one of the factors which has a significant impact on vulture populations (van Beest, van Den Bremer, De Boer, Heitkonig, & Monteiro, 2008) (Parra & Telleria, 2004) and it would be expected to play a role in Griffon Vulture distributions on Crete. The results of this study have confirmed that this does appear to be the case on Crete.

Despite the high abundance of food available on Crete, food availability still has a significant effect on the Griffon vulture foraging distribution. This is in accordance to the literature on the population dynamics of vultures, where food availability is considered to be an important determining factor ((van Beest, van Den Bremer, De Boer, Heitkonig, & Monteiro, 2008)(Parra & Telleria, 2004)(Thiollay, 2006)(Donazar & Fernandez, 1990).

A dynamic modelling study showed that food availability can have a significant role in *gyps fulvus* populations in other locations where the conditions of carcass supply are not so favourable. In Portugal the modelling showed that, when food availability was decreased, an overall decrease in vulture numbers and also breeding pairs was predicted (van Beest, van Den Bremer, De Boer, Heitkonig, & Monteiro, 2008). The situation in Spain also shows food availability to be a limiting factor for Griffon Vulture populations, with an increase in population size positively correlated to changes in livestock abundance (Parra & Telleria, 2004).

The relationship between food availability and foraging distribution occurs despite the very high numbers of livestock reported for Crete which would appear to indicate, through the levels of calculated food surplus, that there is an over abundance of food on Crete. This corresponds to field observations of livestock carcasses in locations close to known Griffon colonies which were not exploited.

The griffon vulture food requirement on Crete is only 1.39% of the calculated total available dead biomass so the significant difference between food inclusive and food exclusive models is unexpected. However, this result is similar to the results from a study on Griffon vultures in Spain. Despite the vultures only consuming 0.5% of the available biomass it was found that food availability was a major limiting factor to the vulture population (Parra & Telleria, 2004).

Considering the large buffer between the amount of dead biomass available and the food requirement of the current population, changes in the food availability seem unlikely to have an immediate impact. If however the subsidisation system was to dramatically change and a subsequent change in livestock and hence dead biomass was to occur, the situation may reach the level where results such as those reported for Spain and Portugal could become relevant in Crete. These results show that changes in livestock abundance have a flow on effect to vulture populations (Parra & Telleria, 2004)(Donazar & Fernandez, 1990)(van Beest, van Den Bremer, De Boer, Heitkonig, & Monteiro, 2008). Subsidisation is currently under threat due to changes within the EU. As the foraging distribution of adult Griffon vultures in summer, and juveniles all year, are influenced by the food availability, livestock distribution changes in the agricultural sector could have a feedback effect on the Griffon vulture populations on Crete.

The economy of Crete is heavily dependent on the European Union (EU) Common Agricultural Policy (CAP) subsidies for income, along with many other Mediterranean countries (Lorent, Sonnenschein, Tsiourlis, Hostert, & Lambin, 2009). This increases the number of livestock relative to the level which would be expected for the environmental conditions, and the livestock number is further decoupled from the environment through the heavy use of additional commercial feed. The potentially inflated livestock figure may explain the very high levels of biomass available. Census data may not reflect real livestock numbers due to inaccurate reporting. This may be due to subsidisation payments. Due to the rough terrain, it is very difficult to verify the data in the areas which have high livestock values.

The model results appear to be very accurate considering that the Griffon Vulture has displayed a high degree of ecological plasticity in other studies (Maraglida, Garcia, & Cortes-Avizanda, 2007) which would indicate that the niche may not be able to be tightly defined. However, for Crete it appears that the areas suitable for foraging for Griffon Vultures are able to be defined using environmental parameters, and, in particular, cloud cover, precipitation and colony distance. This may be due to the sharp environmental gradients on Crete as the landscape rapidly changes from fertile valleys to arid mountains, which are different both in terms of climate and land use. The valleys are generally used for commercial crops and the higher altitudes used for livestock rearing. This may create two clear groups across the variables within MaxEnt and make distinguishing cells where Griffon Vultures are likely to forage more than if the landscape were more homogenous.

The carcasses in the valley may not be available to vultures as they are unable to get airborne again. Also, these are usually small flocks with low mortality rates and the owners usually dispose of the carcasses by burial.

The model was run with numerous permutations with varying results in the probability distribution, although both the training and test AUC were consistently high. The general quality of the models may in part be attributed to the quality and quantity of the presence points. The way the MaxEnt modelling process works is by finding a profile of the parameters and determining how much a given pixel matches this profile.

The variables which contributed the most to the foraging distribution models for Griffon vultures were cloud cover and precipitation. These factors have not been found to be of importance in other studies on griffon vulture distribution, however it is possible that cloud cover is related to visibility, and areas with low visibility are not attractive to Griffon vultures.

The factors considered most important to mortality on Crete were reported as minimum overnight temperatures and the size of flock, as there is a direct relationship with care taken over animals. This translates into fewer deaths due to disease in smaller flocks. Disease has been found to be the leading cause of livestock mortality in other locations ((ILRI, 1983)(Mourad, 2002) so this relationship is important in determining the mortality of the flock.

The livestock mortality rate found on Crete of 4%(Stefanakis, Volanis, Zoiopoulos, & Hadjigeorgiou, 2007) is very low when compared to the rates found in other locations of up to 52% (Mourad, 2002), and also compared to the mortality reported by the livestock owners of up to 15%. In this respect the numbers in this study may be considered to be a conservative estimate of the biomass available for the griffon vultures. However, another factor which may affect the carcass number available to vultures is the burial of carcasses. This is a legal requirement in the EU. However, it is probably not often practised in Crete.

The distance to roads has been found to be a factor in other studies of Griffon Vulture distribution(van Beest, van Den Bremer, De Boer, Heitkonig, & Monteiro, 2008) however the maximum value that distance to road contributed to the model was 3% indicating that on Crete the distance to roads was not so important. This result may be explained by the practise of livestock owners moving the carcasses

close to the houses down to the road and leaving them which was observed during fieldwork. This would balance the desire of the Griffon vultures to avoid the road, with the attraction of available food.

The areas used by Griffon vultures for foraging appears to be seasonal, as the difference between the foraging distributions between summer and winter was found to be significantly different for all pairs except adult food inclusive models. This corresponds with the results reported on the occupation in two colonies in Crete which have a seasonal change in occupation rates (Xirouchakis S. M., Seasonal and daily activity pattern in Griffon Vulture (*Gyps fulvus*) colonies on the island of Crete (Greece), 2007).

This research was limited to goats and sheep which may not accurately account for all the sources of dead biomass available to vultures. In other locations larger carcasses and pigs contribute to the diet of the Griffon vultures. However, in a study of the stomach contents of Griffon vultures on Crete the diet was found to be predominantly composed of sheep, with a secondary contribution of goat ((Xirouchakis S. , 2005). Other species such as cows and pigs did not significantly contribute. Hence, the impact of other species on the foraging distribution of Griffon vultures, considering the abundance of sheep and goats, is considered to be of relatively less importance.

Cloud cover is the main contributing variable in the summer distribution for both adult and juvenile griffon foraging habitats and this was indeed to be expected from observation in the field. Cloud cover reduces the visibility and hence the availability of the carcasses. There is however another explanation for this. The tagged birds were all drawn from the areas around Iraklion for convenience of the researchers. This area has a lower cloud cover so the data may be biased in this respect. The output maps do visually look as expected and the largest colonies are in the Iraklion area, so perhaps the cloud cover is behind the colony size in the Iraklion vicinity.

Another point to consider when interpreting the influence of cloud cover is the very high collinearity with other climatic variables. Due to this, very few climatic variables were left in the model. Therefore cloud cover actually represents the impact of all climatic variables.

Altitude is another variable which cannot be entirely separated from the effect of the climatic variables due to high collinearity. Although altitude undoubtedly plays a role in Griffon foraging behaviour as raptors need height to launch into flight, some

part of the contribution to the model which is assigned to altitude is probably due to climatic factors and the opposite would occur as well.

A limitation of the data is that the worldclim data is missing a tile so there is missing data in the south-western section of Crete. Also, the categorical variables used in the modelling process could not be checked for multicollinearity. However, the results suggest that collinearity may be present. The sensitivity test holding all other variables to an average value indicates that the land cover and geology variables contribute little. However, when the model is compared to these values, some fields are clearly found more frequently than others.

5. Conclusions and Recommendations

The most important factors for livestock mortality on Crete, as reported by livestock owners, are low minimum overnight temperatures and how many animals are owned by a single owner. This was mapped using minimum temperature in the coldest month and livestock holding size as proxies for these variables. The results showed that mortality was weighted highest in the mountainous areas, which also had the highest livestock according to the livestock census data. The livestock census data was redistributed to improve the spatial resolution. Upon visual inspection, the results appeared to be congruent with field observation.

Griffon Distribution can be effectively modelled with a kernel density function using the populations at the colonies as weights and the foraging distance as a smoothing parameter.

The carcass and dead biomass distributions showed very high values overall, with values of up to 1211kg/year for dead biomass in a single 250m cell, which seems excessive. Nonetheless, the mortality estimate was conservative as compared to published material on livestock mortality, and the overall number of livestock is taken from the census data. So, the overall estimate is low.

Even with a low estimate of dead biomass, the 70 000kg/year food requirement is only a small fraction of the total dead biomass. Even with the removal of some carcasses through burial or other disposal methods, the overall food requirement of the Griffon Vultures should easily be met. Uncertainty may be introduced in the form of disposal of the bodies. In this respect, further investigation is recommended.

Adults and Juveniles have fairly similar distributions, although there are some differences between them. Juveniles show an inclination towards proximity to town dumpsites as compared to the adults. The summer and winter distributions are significantly different, although the reasons for this are not apparent from this study. The main factors which influence Griffon Vulture foraging distribution are cloud cover, precipitation and the distance from the colony.

Overall food availability has little influence on Griffon Vulture foraging distributions. The models do not show a significant difference between food included and food excluded scenarios. This may be due to the very high food availability mentioned above.

Whilst *gyps fulvus* is not currently classified as threatened, there are still many mechanisms which can significantly impact on the Griffon vultures on Crete.

Looking at correlations, such as in this study, can be expanded upon by a detailed system dynamics study to understand the effects of future EU policy changes.

Carcass distribution could be better modelled by taking into account the collection of carcasses into the dumpsite and feeding station locations. However, this is unlikely to have an impact on the model as the difference between supply and demand is large.

6. References

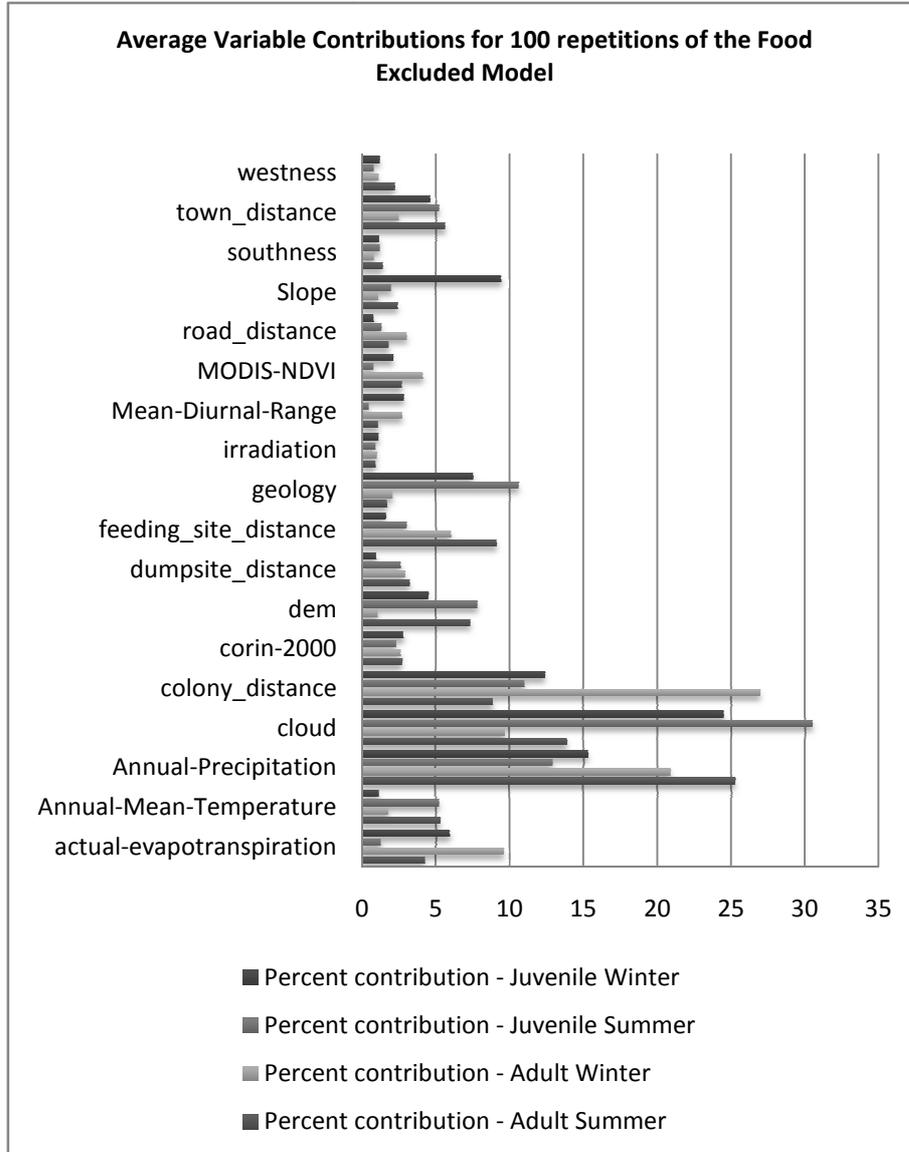
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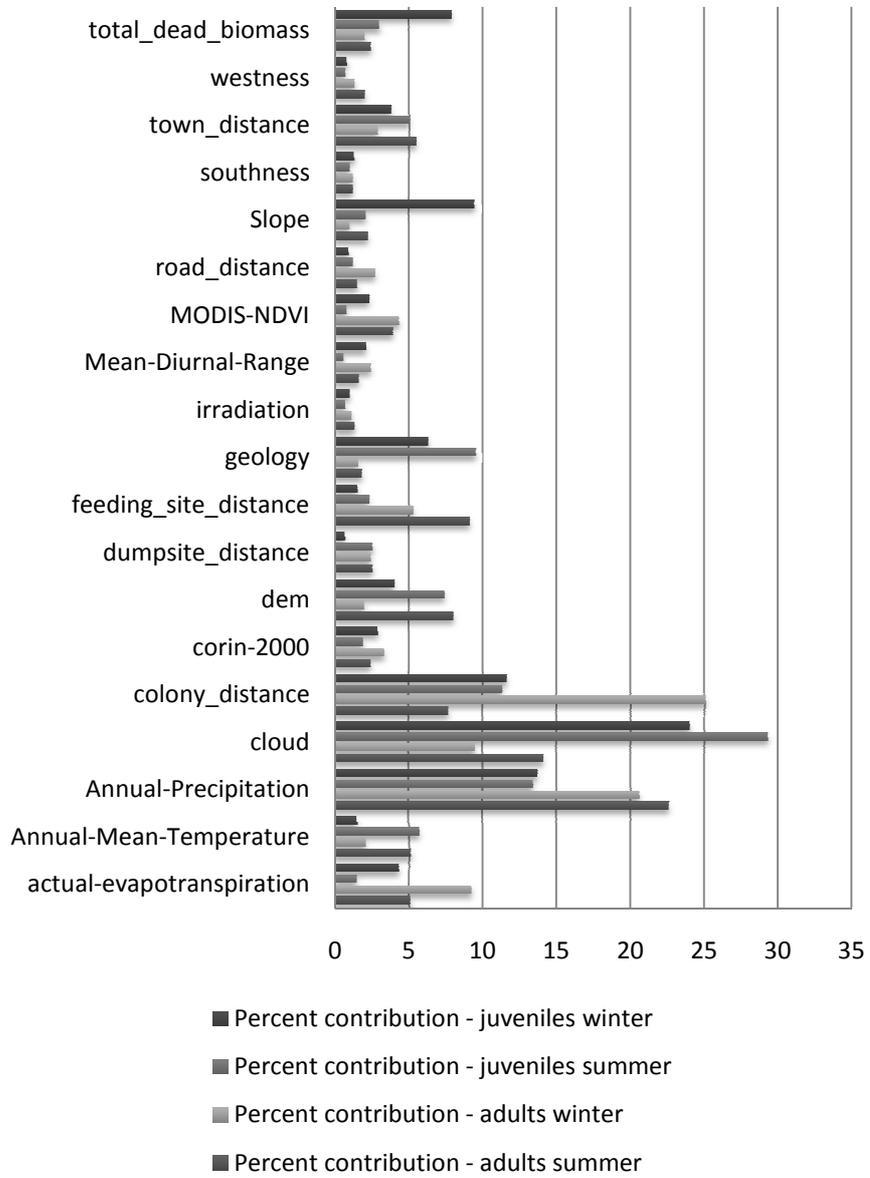
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7. Appendix

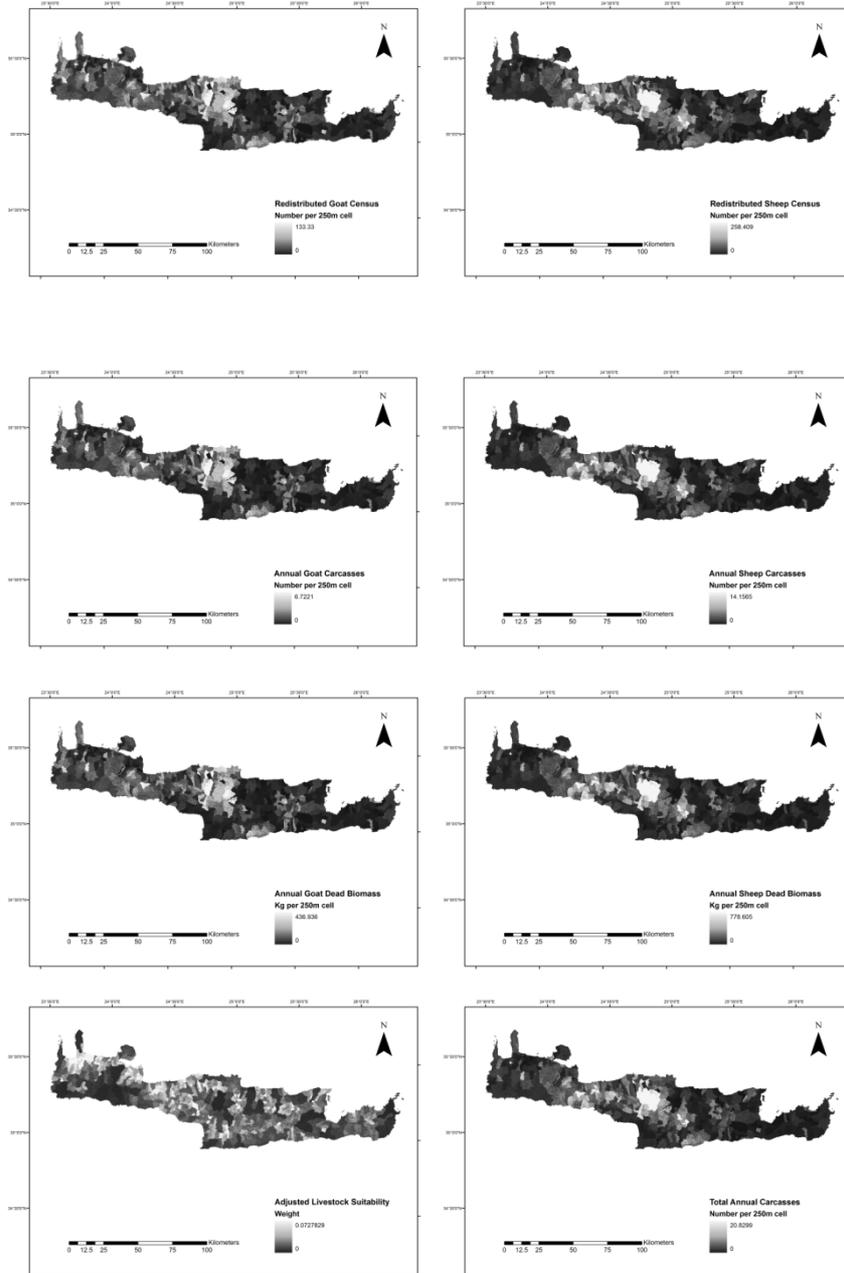
7.1. Contribution of Predictor Variables to Maxent models



Average Variable Contributions for 100 repetitions of the Food Included Model



7.2. Additional Result Maps



Vitsilia vistagi	H2	563299	3900358	3	1
Xiro Oros	F2	545060	3892800	15	11

7.4. Weights for CORINE

COD	Level 1 Class	Level 2 Class	Level 3 Class	Weight
111	Artificial surfaces	Urban fabric	Continuous urban fabric	0
112	Artificial surfaces	Urban fabric	Discontinuous urban fabric	0
121	Artificial surfaces	Industrial, commercial and transport units	Industrial or commercial units	0
122	Artificial surfaces	Industrial, commercial and transport units	Road and rail networks and associated land	0
123	Artificial surfaces	Industrial, commercial and transport units	Port areas	0
124	Artificial surfaces	Industrial, commercial and transport units	Airports	0
131	Artificial surfaces	Mine, dump and construction sites	Mineral extraction sites	0
132	Artificial surfaces	Mine, dump and construction sites	Dump sites	0
133	Artificial surfaces	Mine, dump and construction sites	Construction sites	0
141	Artificial surfaces	Artificial, non-agricultural vegetated areas	Green urban areas	0
142	Artificial	Artificial, non-	Sport and leisure	0

	surfaces	agricultural vegetated areas	facilities	
211	Agricultural areas	Arable land	Non-irrigated arable land	1
212	Agricultural areas	Arable land	Permanently irrigated land	0.5
213	Agricultural areas	Arable land	Rice fields	0
221	Agricultural areas	Permanent crops	Vineyards	0
222	Agricultural areas	Permanent crops	Fruit trees and berry plantations	0.7
223	Agricultural areas	Permanent crops	Olive groves	0.8
231	Agricultural areas	Pastures	Pastures	1
241	Agricultural areas	Heterogeneous agricultural areas	Annual crops associated with permanent crops	0.5
242	Agricultural areas	Heterogeneous agricultural areas	Complex cultivation patterns	0.5
243	Agricultural areas	Heterogeneous agricultural areas	Land principally occupied by agriculture, with significant areas of natural vegetation	0.7
244	Agricultural areas	Heterogeneous agricultural areas	Agro-forestry areas	0.8
311	Forest and semi natural areas	Forests	Broad-leaved forest	0.9
312	Forest and semi natural areas	Forests	Coniferous forest	0.8
313	Forest and semi natural areas	Forests	Mixed forest	0.9

	areas			
321	Forest and semi natural areas	Scrub and/or herbaceous vegetation associations	Natural grasslands	1
322	Forest and semi natural areas	Scrub and/or herbaceous vegetation associations	Moors and heathland	1
323	Forest and semi natural areas	Scrub and/or herbaceous vegetation associations	Sclerophyllous vegetation	1
324	Forest and semi natural areas	Scrub and/or herbaceous vegetation associations	Transitional woodland-shrub	1
331	Forest and semi natural areas	Open spaces with little or no vegetation	Beaches, dunes, sands	0
332	Forest and semi natural areas	Open spaces with little or no vegetation	Bare rocks	0.5
333	Forest and semi natural areas	Open spaces with little or no vegetation	Sparsely vegetated areas	0.8
334	Forest and semi natural areas	Open spaces with little or no vegetation	Burnt areas	0.8
335	Forest and semi natural areas	Open spaces with little or no vegetation	Glaciers and perpetual snow	0
411	Wetlands	Inland wetlands	Inland marshes	0
412	Wetlands	Inland wetlands	Peat bogs	0
421	Wetlands	Maritime wetlands	Salt marshes	0
422	Wetlands	Maritime wetlands	Salines	0

423	Wetlands	Maritime wetlands	Intertidal flats	0
511	Water bodies	Inland waters	Water courses	0
512	Water bodies	Inland waters	Water bodies	0
521	Water bodies	Marine waters	Coastal lagoons	0
522	Water bodies	Marine waters	Estuaries	0
523	Water bodies	Marine waters	Sea and ocean	0
990	UNCLASSIFIED	UNCLASSIFIED	0	0
	D	LAND SURFACE		
995	UNCLASSIFIED	UNCLASSIFIED	UNCLASSIFIED	0
	D	WATER BODIES	WATER BODIES	
999	NODATA	NODATA	NODATA	0