Breeding site selection by bearded vulture (*Gypaetus barbatus*) and Eurasian griffon (*Gyps fulvus*) in the Caucasus

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Abstract

Occupied and unoccupied sites of bearded vulture *Gypaetus barbatus* and Eurasian griffon *Gyps fulvus* were located in the Caucasus (mainly Georgia). Habitat variables related to nest-site characteristics, climate, terrain, human disturbance and food availability were used to construct predictive models of vulture breeding site selection by using a geographic information system (GIS), logistic regression and Bayesian statistical inference. The probability of bearded vulture occupancy of a cliff ledge that was safe from climatic adversity, human disturbance and predation was positively correlated with the following variables measured within a 20-km radius of the ledge: mean elevation, mean slope, the percentage of open areas, mean distance to roads, number of globally threatened wild goats *Capra cylindricornis, C. caucasica* and *C. aegargus*, and annual biomass of dead livestock. The probability of such a cliff ledge being occupied by Eurasian griffon was negatively correlated with annual rainfall at the ledge and positively correlated with the percentage of open areas and annual biomass of dead livestock within 20 km of the ledge. Provided that GIS coverage of the habitat variables is available, these models can be of help in various areas of the Caucasus and elsewhere to predict possible nest occurrence areas, and highlight sites where vultures may occur in the future if the population grows because of conservation or other activities.

Introduction

Throughout parts of Europe and Asia long-term changes in livestock husbandry and management have occurred, and the decline in numbers of wild herbivores has diminished the extent and carrying capacity of habitats that can support vultures. Other factors, including changes in land management, persecution, accidental poisoning and trapping, electrocutions, human disturbance and disease, have helped undermine the stability of many vulture populations (Cramp & Simmons, 1980; Risebrough & Virani, 2000; Virani *et al.*, 2001; Prakash *et al.*, 2002; Pain *et al.*, 2003; Oaks *et al.*, 2004). Feeding stations and reintroduction are seen as stopgap conservation efforts in Europe, and support for pastoral farming systems and traditional methods of carcass disposal might be of long-term benefit (BirdLife International, 1994; Bustamante, 1996; Heredia & Heredia, 1999). Information from quantitative studies of habitat requirements is necessary for designing strategies for the conservation of species, including vultures (Scott *et al.*, 1999; Liberatori & Penteriani, 2001; Scott *et al.*, 2002).

Bearded vultures and Eurasian griffons are two of Europe's most threatened birds (Annex I, EU Wild Birds Directive 79/409/EEC, Appendix II of the Bern Convention, Bonn Convention and CITES). Globally, the bearded vulture is near threatened (Willis, 1994).

To our knowledge no quantitative analyses of habitat requirements of these two species in the Caucasus have been performed. Present-day estimates of bearded vulture and Eurasian griffon in the Caucasus are 83–165 and 285–580 breeding pairs, respectively (BirdLife International, 2004). The protection of these species in the Caucasus is not enforced, and there is no supplementary feeding aimed at their conservation. Fortunately, in the Caucasus these vultures are not considered as pests or competitors, and there is no persecution other than occasional shooting. This study examines breeding site selection by these vultures in the Caucasus, primarily in Georgia.

Our objective was to identify and assess the factors essential for occupancy and successful breeding of these two vulture species in the Caucasus. The models we developed to do so should facilitate the planning and zoning of the developing national park systems in Georgia, and more broadly the conservation of the species in the Caucasus. The models should also contribute to the European Union species action plans and reintroduction programs for these species in Europe.

Materials and methods

Study species

The bearded vulture *Gypaetus barbatus* is a large vulture that specializes in feeding on bones. Pairs nest singly, are strongly territorial and reside in large home ranges (about 200–400 km² containing one or more nests on cliffs (Cramp & Simmons, 1980; Brown, 1988; Heredia, 1991). The mean nearest-neighbor distances are *c.* 11 km in the Spanish Pyrenees (Donázar, Hiraldo & Bustamante, 1993) and 15 km in South Africa (Brown, 1988). Home ranges are traditional and include a foraging range, nest site(s), several roost sites and one or more bone-breaking sites or ossuaries where bones are dropped and cached (Huxley & Nicholson, 1963; Galushin, 1983; Brown, 1988; Margalida & Bertran, 2001). The global distribution of bearded vultures is very large (latitudinally and longitudinally) and conditions in other parts of their range may differ significantly from those found in the Caucasus, affecting the relevance of comparisons.

The Eurasian griffon *Gyps fulvus* is an even larger cliff-nesting vulture. They often nest in colonies that usually comprise less than 20 pairs, but can include more than 100 pairs. They may nest singly, too. The nearest-neighbor distance between pairs depends on the distribution of suitable nest sites on one or more cliffs, rather than territoriality (Cramp & Simmons, 1980). Also, breeding Eurasian griffons are sedentary, but may range over huge areas. Non-breeders are more nomadic (GCCW, 2005; International Center for the Study of Bird Migration, 2005 (Igal/Salam); Camiña, 2004). They feed communally almost exclusively on carrion, especially from medium to large ungulates (Cramp & Simmons, 1980).

Study area

We conducted our study in the Caucasus region, which includes Armenia, Azerbaijan and Georgia, and some parts of the Russian Federation, Turkey and Iran. The Caucasus is a global biodiversity hotspot (Myers *et al.*, 2000). The study area (31 660 km²), which contained part of Georgia and its trans-boundary areas east of 42° longitude (Fig. 1), was surveyed for nesting bearded vulture and Eurasian griffons between 1994 and 2003. Surveys were conducted year-round as part of a vulture-monitoring program by the Georgian Center for the Conservation of Wildlife (GCCW), Tbilisi, Georgia. Most valleys and gorges within the study area were searched by a four-wheel drive vehicle, on horse-back and on foot. Nests were found and monitored using telescopes. Elevation in the study area varied from 0 to 5200 m a.s.l. and annual rainfall from 300 to 4500 mm.

Analytical approach

Nest-site selection was examined by comparing habitat variables at nest sites occupied by vultures with those at unoccupied, but apparently appropriate, sites (Fig. 1). These variables used were based on documented species–habitat associations (Cramp & Simmons, 1980), our field experience and models developed for similar species (e.g. Donázar *et al.*, 1993; Liberatori & Penteriani, 2001).

Suitable, but unoccupied, sites (hereafter, 'unoccupied sites') were identified based on the protection they offered from weather, human disturbance and predation, and their distance from occupied sites. Nest-site characteristics, elevation, slope, aspect, proximity to roads and populated areas (Table 1) were measured at all known nests of each species that had been successful at least once in the past 10 years
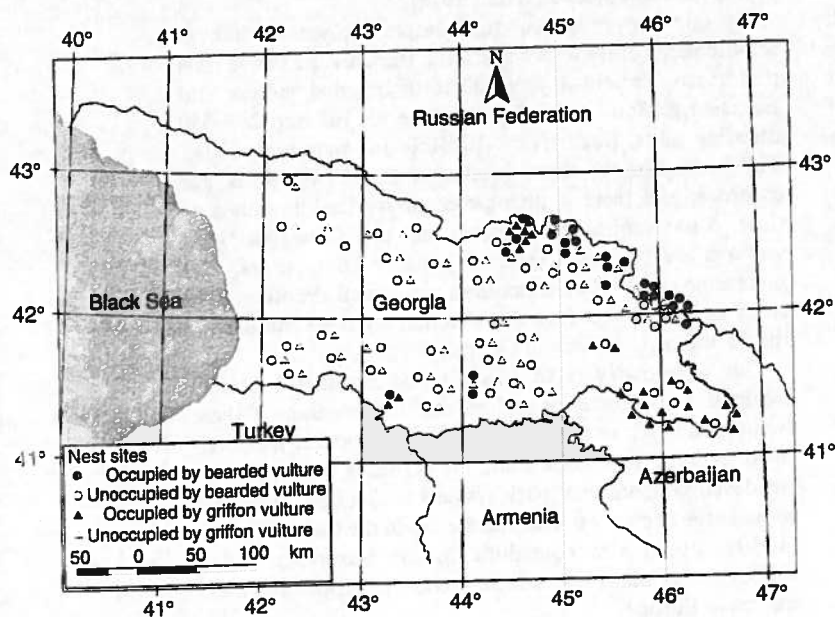

Figure 1 The study area and distribution of occupied and unoccupied sites used for modeling.

Table 1 Habitat variables used in the analyses of vulture breeding-site selection

Variable	Description	Method of measurement
Nest-site characteristics		
h_1	Distance (m) from top of nest niche to nearest place at top of cliff accessible to potential terrestrial predators	Rappelling; photographs of known scale
h_2	Distance (m) from bottom of nest niche to nearest place at bottom of cliff accessible to potential terrestrial predators	Rappelling; photographs of known scale
W	Distance (m) between the nest and the nearest GPS point across valley from the nest at the same elevation from where the nest could be fully seen	GPS and GIS
AV	Number of avalanches at the site in the past 20 years based on physical evidence and local reports	Interviews and site-visits
BV, GV, GE, P, R	Distances (m) to the nearest nests of cliff nesting birds whose aggressiveness and territoriality might affect cliff occupancy: bearded vulture *Gypaetus barbatus*, Eurasian griffon *Gyps fulvus*, golden eagle *Aquila chrysaetos*, peregrine falcon *Falco peregrinus*, and raven *Corvus corax*, respectively	GPS and GIS
(a) Climate		
Elevation	Elevation (m) above sea level at a scale of 20×20-m plots	GIS
MeanElevation	Mean elevation (m) within a 20-km radius, averaged from a 20-m grid interpolated from 40-m elevation contours	GIS
Rainfall	Annual rainfall (mm) at a scale of 20×20-m plots	GIS
MeanRainfall	Mean annual rainfall (mm) within a 20-km radius, averaged from a 20-m grid interpolated from 200-mm rainfall contours	GIS
Sunlight	Hours of sunlight per year measured at a scale of 20×20-m plots	GIS
MeanSunlight	Mean annual hours of sunlight within a 20-km radius, averaged from a 20-m grid interpolated from 100-h sunlight contours (h)	GIS
(b) Terrain		
Slope	Steepness (°) at a scale of 20×20-m plots	GIS
MeanSlope	Mean slope (°) within a 20-km radius, averaged from a 20-m slope grid	GIS
Aspect	Bearing from the nest to the point where W (above) measured, categorized as NE, NW, SE or SW	GPS
Openland	Percentage of open areas within a 20-km radius	GIS
(c) Human disturbance		
HumPop	Number of humans living within a 20-km radius	Existing accounts and interviews
DisPop	Non-Euclidean over-land (actual) distance (m) to the nearest populated area at a scale of 20×20-m plots	GIS
MeanDisPop	Mean distance (km) to populated areas within a 20-km radius, averaged from a 20-m grid	GIS
DisRoad	Non-Euclidean over-land (actual) distance (m) to the closest point on road at a scale of 20×20-m plots	GIS
MeanDisRoad	Mean distance (km) to roads within 20-km radius, averaged from a 20-m grid	GIS
(d) Food availability		
Capra	Number of wild goats including East Caucasian tur *Capra cylindricornis*, West Caucasian tur *C. caucasica* and bezoar *C. aegargus* within a 20-km radius	Data on densities and distribution ranges
Chamois	Number of chamois *Rupicapra rupicapra* within a 20-km radius	Data on densities and distribution ranges
Snowcock	Number of Caucasian and Caspian snowcocks *Tetraogallus caucasicus* and *T. caspius* within a 20-km radius	Data on densities and distribution ranges
Grouse	Number of Caucasian grouse *Tetrao mlokosiewiczi* within a 20-km radius	Data on densities and distribution ranges
DeadStock	Annual biomass of dead livestock (tons per year) calculated from numbers, mortality rates and weights in each populated area within a 20-km radius (Table 3)	Interviews
Shrine	Number of shrines and temples where livestock are sacrificed within a 20-km radius	Site visits

GIS, geographic information system; NE, north-east; NW, north-west; SE, south-east; SW, south-west.

(28 bearded vulture and 34 Eurasian griffon nests). The measurements were made while climbing into nests, from photographs of known scale and from 1:50 000 digital topographic maps. The ranges of these measurements were then used to identify unoccupied sites for each species (Table 2).

We compared 25 nest sites occupied by bearded vultures in 2001–2003 with 50 unoccupied sites >9 km (minimum

Table 2 Ranges (mean ± SD) of variables measured at occupied vulture nest-sites, used to define unoccupied sites (these variables were not used in model estimations

Variables	Bearded vulture Gypaetus barbatus (n=28)	Eurasian griffon Gyps fulvus (n=34)
h_1	8–110 (44.16 ± 38.28)	9–110 (56 ± 33.23)
h_2	8–150 (89.5 ± 36.8)	11–150 (92.3 ± 35.9)
W	150–2 000 (900 ± 310)	150–2 000 (1 320 ± 402)
AV	0	0
BV	8 645–71 140 (22 581 ± 20 590)	993.8–76 774 (43 896 ± 27 443)
GV	993.8–76 774 (43 896 ± 27 443)	3–14 140 (921 ± 3022)
GE	2 285.1–60 770 (12 241 ± 14 190)	7 102.4–84 435 (36 903 ± 32 553)
P	260.2–25 758 (8 670.5 ± 7 507)	231.8–43 039 (12 205 ± 15 363)
R	101–7 001.8 (2 781 ± 2 152)	20–4 078 (1 185.2 ± 1 210)
Elevation	700–2 310 (1 883 ± 269.2)	442.7–2 300 (1 383.9 ± 656.5)
Slope	21.8–53.6 (37.4 ± 10)	15.10–45.7 (24.1 ± 11.4)
Aspect	NW–SE	SE–SW
DstRoad	295–10 423 (2 507.5 ± 2 932.7)	295–1 782.1 (750.6 ± 553.1)
DstPop	746.7–9 754.3 (3 838.7 ± 2 995.8)	349.3–11 249 (3 385 ± 3 474)

NW, north-west; SE, south-east; SW, south-west.

nearest-neighbor distance for bearded vultures, Table 2) from one another and from occupied nest sites. Because Eurasian griffons are colonial, we compared 25 nests occupied in 2001–2003 that were >2 km distant from one another with 50 unoccupied sites. To derive models of breeding site selection for both species, habitat variables other than the ones used to identify unoccupied sites were measured both at the level of a nest-site location and within a 20-km radius of a nest site (Table 1). The 20-km distance was used because it was the extent to which a radio-marked territorial female bearded vulture ranged from her nest in 2002 and 2004 (A. Gavashelishvili, unpubl. data). This value was also used for assessing Eurasian griffon nest-site occupancy, but, because of their lack of territoriality, was to some extent arbitrary.

Habitat variables

Variables related to nest-site characteristics, climate, terrain, human disturbance and food availability were considered (Table 1). Climate data were extracted from Khatiashvili, Ushveridze & Kobakhidze (1989). Terrain data were measured from updated digital topographic maps (source: 1:200 000, Headquarters of Geodesy and Cartography under the Council of Ministers of the USSR, 1968, Facility No. 11) using ArcView v.3.3 GIS software (ESRI Inc., Redlands, CA, USA) and a Garmin Etrex 12 Channel GPS unit (Garmin Corp., Ulathe, KA, USA).

Prey remains were collected from nests and their immediate vicinity. Information on diet from these collections, published accounts (Zabelin, 1976; Komarov & Veinberg, 1981; Veinberg et al., 1983; Vitovich, 1983; Komarov, 1985; Abuladze, 1989; Brown & Plug, 1990; Thibault, Vigne & Torre, 1993) and observations made by local hunters were used to identify the species that were most important to vultures in the Caucasus.

Livestock (sheep, goat, pig, cattle, horse and donkey) and human numbers were provided by the Ministry of Statistics of Georgia for populated areas in the Georgian portion of the study area. Interviews of local inhabitants (in 2001–2003) in remote areas of Georgia and in the trans-boundary portions of the study area provided information where published data were unavailable. In interviews in both remote and populated areas, we inquired about the number of different livestock in three age categories (juvenile, immature and adult), the mean weight of individuals and the rate of mortality in each of these categories. We interviewed 100 farmers and used the average of their estimates of livestock weights and mortality rates as inputs into our analyses.

In the study area, all livestock except about half of the pigs were extensively farmed, and dead domestic animals were dumped away from populated areas. Total annual biomass for each livestock species that was potential food for vultures was calculated for each populated area by summing the products of the total number, mean annual mortality and mean weight of each age category (Table 3).

Transhumance (i.e. seasonal altitudinal movements of extensively husbanded livestock) is practised in the Caucasus, and tens of thousands of livestock, predominantly sheep, are moved in May and September over long distances (>50 km) between winter and summer pastures (Agladze, 1964; Zhghenti et al., 1986). As a result, transhumant livestock spends only about half the year on summer and the other half on winter pastures. Therefore, to more accurately estimate the annual biomass of dead livestock within a 20-km radius of an occupied or unoccupied nest site, the mortality rate of the transhumant portion of livestock population was halved. The total biomass of carcasses was the sum of the biomass from resident and transhumant livestock.

In the Caucasus, pagan deities are still worshipped, particularly in the highlands, and livestock are sacrificed, mostly in July–mid September and Christmastime–New Year (A. Gavashelishvili, unpubl. data). Remains of
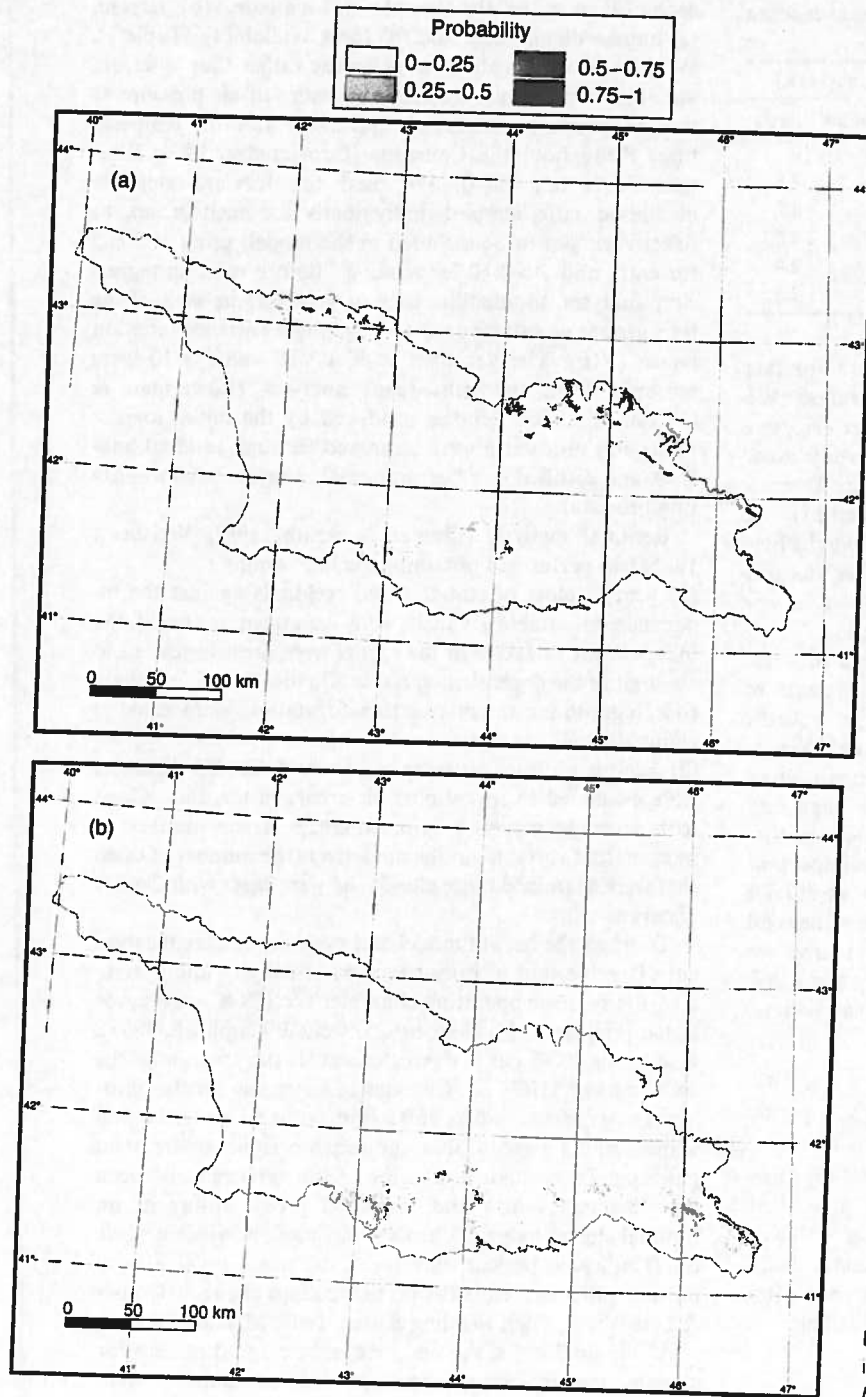
Figure 2 Prediction maps for vulture nest sites in Georgia: (a) bearded vulture *Gypaetus barbatus*, and (b) Eurasian griffon *Gyps fulvus*.

sacrificed animals are consumed by vultures and other scavengers, so we included the location of sacrificial sites in our analysis.

The numbers of wild animals that were a potential food source were calculated from their densities (Kutubidze, 1955, 1961; Ponkova, 1967; Kuliev, 1981; Magomedov *et al.*, 2001; Gokhelashvili, Kerry & Gavashelishvili, 2003) and range extent. We derived ranges for each wild animal

species using the method employed for East Caucasian tur *Capra cylindricornis* (Gavashelishvili, 2004).

Although vultures sometimes feed on the carcasses of red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, brown bear *Ursus arctos* and wild boar *Sus scrofa* (our observations; Komarov & Veinberg, 1981; Veinberg *et al.*, 1983; Vitovich, 1983; Thibault *et al.*, 1993), these animals were mainly confined to dense woodland in our study area, and

Table 3 Livestock characteristics in the Caucasus, used to calculate annual biomass of dead animals

Livestock	Mean weight (kg)			Mean annual mortality (%)		
	Juvenile	Immature	Adult	Juvenile	Immature	Adult
Sheep	10	20	30	21	5	6
Goat	10	20	30	16	4	4.8
Pig	19	60	90	14	3.4	4.2
Cattle	65	200	300	8.2	2.5	3.1
Horse	86	267	400	6.2	2	2.4
Donkey	20	60	80	4.1	1	2.3

their carcasses were rarely available to vultures. For this reason, we did not include these species in our analysis. We also excluded fox *Vulpes vulpes* and hare *Lepus europeus* because of their even distribution across the study area. Because we think that carcass availability in late December–April (Cramp & Simmons, 1980; Gavashelishvili & Javakhishvili, 2002; Gálvez, Gavashelishvili & Javakhishvili, 2005) is most important in determining whether vultures establish a breeding site, we excluded from our analyses species that migrate over large distances or hibernate.

Bearded vultures bathe in water and mud high in ferric oxide or rub themselves on iron-rich rocks (Brown & Bruton, 1991; Houston, Hall & Frey, 1993; Frey & Roth-Callies, 1994; Caussimont, Hunot & Mariette, 1995; Xirouchakis, 1998), a behavior thought to play a role in reproduction (Arlettaz *et al.*, 2002), maybe through signaling dominance (Negro *et al.*, 1999, 2002). Initially, we hypothesized that the presence of these bathing places was important to bearded vulture nest-site choice, but ultimately we did not consider this factor because bathing places occurred near all occupied and unoccupied sites. For the same reason we excluded from our analysis the presence of stony areas that could possibly be used by bearded vultures to break bones.

Statistical treatment

Statistical analyses were performed using SPSS v.11 for Windows (SPSS Inc., Chicago, IL, USA).

Binomial logistic regression was used to model breeding habitat requirements for each species as the dependent variable (occupied nest site = 1 or unoccupied site = 0) was dichotomous (Hosmer & Lemeshow, 1989; Menard, 2002). Logistic regression estimates parameters (coefficients) after transforming the dependent variable into a logit variable:

$$\ln[p/1-p] = B_0 + B_1 X_1 + B_2 X_2 + \cdots$$

where ln is the natural logarithm, p is the probability of obtaining a positive response (in our case, nest presence), B_0, B_1, B_2, ... are parameters to be estimated from the observed data, and X_1, X_2, ... are the independent (i.e. explanatory) variables.

Because the number of independent variables in relation to a sample size increases the likelihood of multicollinearity and the possibility that some variables would be significant just by chance, we divided habitat variables into four groups so that there was no more than one independent variable for each 10 cases in the sample: (a) climate, (b) terrain, (c) human disturbance and (d) food availability (Table 1). We considered elevation as a climatic rather than a terrain variable, because it is a reliable measure of air pressure as well as minimum, maximum and mean monthly temperatures throughout the Caucasus (Dzotsenidze, 1964; Khatiashvili *et al.*, 1989). We used the forward stepwise likelihood ratio method, individually for each group, to select variables to be included in the model, using $P < 0.05$ for entry and $P > 0.10$ for removal. Before running regression analyses, multicollinearity of variables in each of the four groups was diagnosed by checking a variance inflation factor (VIF). The variables with a VIF value > 10 were removed from the subsequent analyses (Bowerman & O'Connell, 1990). Models produced by the initial logistic regression procedure were improved through residual analysis, and distilled to a best-fit model using a model evaluation procedure.

Residual analysis (Draper & Smith, 1981; Weisberg, 1985) was performed obtaining the following:
(1) Scatter plots of standardized residuals against the independent variables, which were examined to see if the independent variables in the model were linearly related to the logit of the dependent variable. Quadratic, cubic, square root, logarithmic and inverse transformations were tested to eliminate nonlinearity.
(2) Scatter plots of leverage values and Cook's distances were examined to reveal possible errors in the data. Cases with leverage values $> 2p/n$, where p is the number of independent variables in the model, n is the number of cases that were examined more closely, as were cases with Cook's distances > 1.

To select the best-fit model and optimize its classification cut-off value that equally balanced sensitivity and specificity, the receiver operating characteristic (ROC) curve was tested (Hanley & McNeil, 1982; Zweig & Campbell, 1993). One of the ROC curve characteristics is the area under the ROC curve (AUC). AUC values of 1 suggest the classification to be correct, values of 0 suggest it to be incorrect, and values of 0.5 suggest that the scheme is no better than guessing. To evaluate a measure of the agreement between the observed values and predicted group values at an optimal cut-off value, Cohen's κ was used, in which a value of 1 indicates perfect agreement, whereas a value of 0 indicates that agreement is no better than chance (Hosmer & Lemeshow, 1989; Fielding & Bell, 1997; Menard, 2002).

At the final stage, the obtained a, b, c and d models for climate, terrain, disturbance and food availability were combined using Bayesian statistical inference that is promoted in contexts of conservation and resource management (Crome, Thomas & Moore, 1996; Ellison, 1996; Ludwig, 1996; Taylor *et al.*, 1996; Wolfson, Kadane & Small, 1996). So,

$$P_{abcd} = P_a P_b P_c P_d / [P_a P_b P_c P_d + (1 - P_a)(1 - P_b)(1 - P_c)(1 - P_d)]$$

where P_a, P_b, P_c and P_d are probabilities obtained from variables associated with climate, terrain, disturbance and food availability, respectively, and P_{abcd} is the overall probability.

We assessed the power and accuracy of the final Bayesian model using the ROC and Cohen's κ. In the final evaluation procedure, when sensitivity and specificity were balanced equally, we used the leave-one-out cross-validation [i.e. fitting the model with all observations minus one and predicting for this observation, and repeating this procedure for all observations (Scott *et al.*, 2002)]. Because complete sets of the variables included in the final model for the bearded vulture were not available for other nests in the Caucasus, we only tested the final model for the Eurasian griffon, employing additional sites located in Georgia, but not used in the estimation of the model. The additional sites or testing sites included the locations of 30 occupied and 30 unoccupied sites that were spaced > 2 km from each other and the sites used in the model estimation. The testing sites were overlaid onto an optimized probability grid of the model to extract values for each testing location. The extracted values and those of the testing dataset were then summarized in an error matrix, from which four measures of accuracy were calculated: overall accuracy, sensitivity, specificity and the κ statistic (Fielding & Bell, 1997).

Results

Nest-site characteristics

Table 2 summarizes the characteristics of occupied nest sites. Most bearded vulture nests faced north-west or south-east (13 north-west; 11 south-east; three south-west; one north-east), whereas most Eurasian griffons nested on south-east and south-west facing cliffs (23 south-east; two north-west; eight south-west; one north-west). None of the nests was particularly liable to avalanche.

Bearded vulture

Considering climatic variables only, the best-fit model of bearded vulture breeding-site selection included mean elevation (Table 4). At its optimal classification cut-off, the model correctly classified 76% of occupied and 82% of unoccupied sites. Overall, the model correctly classified 80% of all sites.

The best-fit model based on terrain variables included mean slope and open land. At its optimal classification cut-off, it correctly classified 77% of occupied and 86% of unoccupied sites. Overall, the model correctly classified 83% of all sites.

The only human disturbance variable selected was mean distance to roads. At its optimal classification cut-off, the model correctly classified 81% of occupied nest sites and 84% of unoccupied sites. Overall, the model correctly classified 83% of all sites.

The regression procedure suggested that the most important food variables were the number of wild goats and the amount of dead livestock per year. The most widely dis-

Table 4 Models for bearded vulture *Gypaetus barbatus* breeding site, using binomial logistic regression

Model	Parameter estimate	SE	Wald	P
Climate				
MeanElevation	0.003	0.001	10.510	0.001
Constant	−5.872	1.800	10.640	0.001
2 Log likelihood	−32.601			
Nagelkerke R^2	0.543			
d.f.	1			
AUC	0.891	0.052		<0.001
Optimal classification cutoff	0.4			
Cohen's κ	0.573	0.134		<0.001
Terrain				
MeanSlope	0.202	0.064	9.984	0.002
Openland	0.065	0.025	6.927	0.008
Constant	−8.486	2.436	12.133	<0.001
2 Log likelihood	−31.306			
Nagelkerke R^2	0.569			
d.f.	1			
AUC	0.907	0.049		<0.001
Optimal classification cutoff	0.4			
Cohen's κ	0.622	0.129		<0.001
Human disturbance				
MeanDstRoad	0.804	0.244	10.814	0.001
Constant	−2.755	0.802	11.800	0.001
2 Log likelihood	−35.513			
Nagelkerke R^2	0.481			
d.f.	1			
AUC	0.837	0.073		<0.001
Optimal classification cutoff	0.4			
Cohen's κ	0.632	0.126		<0.001
Food availability				
Capra	0.020	0.073	7.114	0.008
DeadStock	0.033	0.013	6.474	0.011
Constant	−12.642	4.709	7.206	0.007
2 Log likelihood	−14.43			
Nagelkerke R^2	0.842			
d.f.	1			
AUC	0.973	0.024		<0.001
Optimal classification cutoff	0.4			
Cohen's κ	0.893	0.073		<0.001
Bayesian combination of the above models				
AUC	0.960	0.026		<0.001
Optimal classification cutoff	0.4			
Cohen's κ	0.730	0.113		<0.001

AUC, area under the receiver operating characteristic curve.

tributed wild goat was the East Caucasian tur. The model, at its optimal classification cut-off, correctly classified 93% of occupied and 96% of unoccupied sites. Overall, the model correctly classified 95% of all sites.

The residual analyses did not reveal influential points in the models that performed significantly better than chance. The ROC analysis suggested excellent performance of the final Bayesian model, which correctly classified 88% of occupied nest sites and 91% of unoccupied sites. Overall, the model correctly classified 90% of all sites and 89% of the cross-validated cases. Figure 2 shows the results of the application of the final model to the entire territory of Georgia.

Eurasian griffon

The best-fit model suggested annual rainfall around a nest site to be more important than the other climate variables (Table 5). The model, at its optimal classification cut-off, correctly classified 85% of occupied and 82% of unoccupied sites. Overall, the model correctly classified 83% of all sites.

Of terrain variables, the amount of open areas explained best the probability of cliff occupancy. The model, at its optimal classification cut-off, correctly classified 93% of occupied nest sites and 90% of unoccupied sites. Overall, the model correctly classified 91% of all sites.

Table 5 Models for Eurasian griffon *Gyps fulvus* breeding site, using binomial logistic regression

Model	Parameter estimate	SE	Wald	P
Climate				
Rainfall	−0.008	0.003	8.866	0.003
Constant	5.285	1.836	8.282	0.004
2 Log likelihood	−33.762			
Nagelkerke R^2	0.540			
d.f.	1			
AUC	0.858	0.058		<0.001
Optimal classification cutoff	0.5			
Cohen's κ	0.652	0.118		<0.001
Terrain				
Openland	0.117	0.038	9.526	0.002
Constant	−9.310	3.049	9.321	0.002
2 Log likelihood	−32.078			
Nagelkerke R^2	0.573			
d.f.	1			
AUC	0.909	0.054		<0.001
Optimal classification cutoff	0.5			
Cohen's κ	0.799	0.095		<0.001
Food availability				
DeadStock	0.010	0.003	9.015	0.003
Constant	−3.478	1.065	10.664	0.001
2 Log likelihood	−43.313			
Nagelkerke R^2	0.327			
d.f.	1			
AUC	0.772	0.087		0.004
Optimal classification cutoff	0.3			
Cohen's κ	0.413	0.140		0.006
Bayesian combination of the above models				
AUC	0.960	0.029		<0.001
Optimal classification cutoff	0.5			
Cohen's κ	0.842	0.088		<0.001

AUC, area under the receiver operating characteristic curve.

Human disturbance variables failed to explain the probability of cliff occupancy by Eurasian griffons, and were not included in the final Bayesian model.

When food variables were considered, the amount of dead livestock per year explained best the probability of cliff occupancy. The model, at its optimal classification cut-off, correctly classified 73% of occupied and 70% of unoccupied sites. Overall, the model correctly classified 71% of all sites.

The residual analyses did not reveal influential points in the above models that performed significantly better than chance. The ROC analysis suggested an excellent performance of the final Bayesian model, which correctly classified 86% of occupied and 89% of unoccupied sites. Overall, the model correctly classified 88% of all sites and 87% of the cross-validated cases. Measures of predictive accuracy calculated from an error matrix of the model-predicted values and the observations not used in the estimation of the model are summarized in Table 6. Figure 2 shows the results of the application of the final model to the entire territory of Georgia.

Discussion

Nest-site characteristics

North-west and south-east aspect preferences shown by bearded vultures may be accounted for by wind patterns or interspecific competition with other cliff nesters, especially golden eagles *Aquila chrysaetos* and Eurasian griffons (Fernandez & Donázar, 1991; Margalida & Garcia, 1999), and this may influence aspect choice.

Bearded vulture

The maximum observed nesting elevation (2310 m, Table 2) and the positive response of the model to elevation range below this value are consistent with findings by Donázar *et al.* (1993), indicating that the species avoids higher elevations because of harsh climate and low food availability, and lower elevations perhaps because of human disturbance.

Table 6 Measures of predictive accuracy calculated for the final model of Eurasian griffon *Gyps fulvus* using validation dataset

Measure	Calculation	Value
Overall accuracy	$(a+d)/n$	0.98
Sensitivity	$a/(a+c)$	0.97
Specificity	$d/(b+d)$	1
κ statistic	$[n(a+d)-[(a+b)(a+c)$ $+(c+d)(d+b)]/[n^2$ $-(a+b)(a+c)$ $+(c+d)(d+b)]$	0.97 $(P<0.001)$

$n=(a+b+c+d)$, where *a* is the number of presence cases correctly predicted by the model; *b* the number of absence cases where the model predicted presence; *c* the number of presence cases where the model predicted absence; *d* the number of absence cases correctly predicted by the model.
n of presence =30, *n* of absence =30.

Our model suggests a positive response of the bearded vulture to the extent of open areas. All large, old world vultures need open landscapes (Cramp & Simmons, 1980), which offer better foraging conditions to vultures that detect food by sight. Also, openness (i.e. low and sparse vegetation cover) is associated with better soaring conditions (Stull, 1988).

Our result that mean slope (ruggedness) is important to the bearded vulture agrees with that of Pennycuick (1972), Hiraldo, Delibes & Calderon (1979), Brown (1988), Mundy et al. (1992) and Donázar et al. (1993), and might be related to ease of flight [much more than other vultures, bearded vultures fly close to the ground in rugged areas using dynamic updrafts (Cramp & Simmons, 1980)] or availability of prey (rugged terrain is more hazardous for animals). On balance we judge ease of flight provided by a rugged terrain as being more important than increased food availability, because bearded vultures are rarely recorded in flat lands where food is available (especially in light of their specialization on bones, which means they do not compete with griffons). Rugged terrain also provides snow-free rocks and Scree slopes that are used by bearded vultures for catching food and breaking bones (Boudoint, 1976; Brown, 1988; Heredia, 1991).

Our analysis indicates that bearded vultures avoid areas where road network density (~ 1/mean distance to roads) is high. We accept that the pattern of road distribution and their use and the type of food that is available may affect food availability. However, road density also accounts, to some extent, for development and consequent disturbance that may affect food availability for bearded vultures. Breeding bearded vultures generally forage perhaps within 20 km of their nests ($\sim 1257 \text{ km}^2$) in the Caucasus (A. Gavashelishvili, unpubl. data) and even smaller areas of $300-700 \text{ km}^2$ in South Africa (Brown, 1988), and human disturbance within these distances must be critical for cliff occupancy. Road network density affects bearded vulture breeding success in Spain (Donázar et al., 1993).

The remains of wild goats and livestock were most important in supporting breeding bearded vultures. During field-work to survey for bearded vultures, we also collected pellets at nests, and about 60% of pellets ($n = 140$) from 14 pairs contained remains of Turs. In our study area in the winter, the entire population of Chamois descends into lower lying woodlands, whereas wild goats remain in open, rugged areas throughout the year. This behavioral difference explains the relative unimportance of Chamois for the bearded vulture. Although bearded vultures may prey upon snowcocks and grouse (Zabelin, 1976; Komarov & Veinberg, 1981; Abuladze, 1989) and their eggs, these items appear to be an occasional rather than a regular and important source of food (A. Gavashelishvili, unpubl. data). Because sacrificing animals is highly seasonal in the study area and, according to our own observations, does not supply food to vultures during the most critical period, winter, it seems insignificant for cliff occupancy.

Eurasian griffon

Cliff occupancy by Eurasian griffon in the Caucasus is closely associated with low annual rainfall, which agrees with data from elsewhere (Cramp & Simmons, 1980), and this preference may be related to griffon flight strategies. Eurasian griffons often soar in thermals (Bögel, 1996), whose strength and regularity is negatively correlated with the amount of moisture in the ground, irregularities in the land surface and strength of wind, but positively correlated with the amount of sunlight (Stull, 1988). In the study area, high amounts of sunlight do not necessarily correspond to low ground moisture, because many of the sunniest areas are covered in dense woodland or are cultivated. Low annual rainfall correlates well with both high amounts of sunlight and low ground moisture, and where this occurs, soaring conditions for vultures, especially Eurasian griffons, are best. Because even small increases in energy expenditure (or decreases in density of carcasses) can have a large impact on the foraging range of Gyps vultures (Ruxton & Houston, 2002), soaring flight is essential. The model indicates the positive correlation of Eurasian griffon breeding sites with open areas, and as with bearded vulture, this is probably related to easier carcass detection and better soaring conditions.

Our study suggests that as long as the nest site is safe from direct human approach, Eurasian griffons are less affected than bearded vultures by human disturbance. Moreover, their diet comprises mostly food from domesticated animals, a feature also found in Spain (Camiña, 2004). Whole-colony energy requirements of nesting Eurasian griffons may result in preference for livestock or herd animals. Before extensive overhunting and overgrazing (Ministry of Environment of Georgia, Tbilisi, pers. comm.), it is likely that Eurasian griffons fed more upon carcasses from wild animals, especially goitered gazelle Gazella subgutturosa, which occurred in large numbers in eastern Georgia, but these have depleted and Eurasian griffons are now more tied to places where food is regularly available because of mortality of livestock. A comparison of the relative productivity of two colonies of Eurasian griffons in Georgia illustrates the importance of livestock rather than wild prey for this species. At a lowland colony ($< 800 \text{ m a.s.l.}$), where large numbers of wintering livestock (mostly sheep) occur in the beginning of a nestling period, but which are moved to distant pastures during May through September, 29 griffon pairs rear < 0.5 fledgling per pair laying eggs. In contrast, at a highland colony ($> 1500 \text{ m a.s.l.}$), where Eurasian griffons start their breeding season in the presence of small numbers of year-round livestock, and whose numbers then increase greatly in May with the arrival of summering livestock, the number of pairs that lay eggs is much smaller, 15 pairs, but their breeding success was > 0.8 fledgling per pair laying eggs (Gavashelishvili & McGrady, 2003).

Conservation implications

Provided that habitat information is available and can be used within a GIS, the models that we developed can be applied elsewhere in the Caucasus to predict possible nest occurrence, and highlight sites where the vultures may occur in the future. Our models can be used to help prioritize sites

for conservation efforts by identifying areas where management of factors such as human disturbance and food supply are likely to have the greatest effect. The models suggest that efforts to stabilize or increase the breeding populations of the vultures in the region should consider the adverse effects of growth of populated areas and expansion of the road network, and the positive influence of the traditional ways of carcass disposal (see also Camiña, 2004) and the protection of wild goat populations that have poor conservation status (see IUCN, 2004). In particular, our models could contribute to a scheme of zoning infrastructure development, hunting, land use and recreation/tourism to favor vultures. In Georgia the importance of a grid-based zoning system for providing secure areas for some species, including bezoar goat, has been demonstrated in the proposed Tusheti National Park (Gokhelashvili et al., 2002).

Also, in the Caucasus where the terrain and climate are extreme and the cost of wildlife censuses is high, our models can enable resource managers and conservationists to better estimate vulture populations, manage and apply conservation efforts efficiently.

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