

Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture

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Summary

1. Species undergoing reintroduction offer a unique opportunity for clarifying their specific niche requirements because they are likely, if sufficiently mobile, to colonize the most suitable habitats first. Information drawn from the individuals released first might thus be essential for optimizing species' policy as reintroductions proceed.
2. Bearded vultures were extirpated from the European Alps about a century ago. An international reintroduction programme using birds reared in captivity was launched in 1986; up to 2003, 121 individuals had been released at four different locations. Subsequent dispersion throughout the range has been far from homogeneous, resulting in a clumped occurrence of the first breeding pairs within three main zones that do not necessarily coincide with release areas.
3. In order to discern ecological requirements we performed a geographical information system (GIS) analysis of bearded vulture sightings collected in Valais (Swiss Alps) from 1987 to 2001. This area harbours no release site, is situated in the core of the Alpine range and has been visited by birds from all four release points.
4. During the prospecting phase (1987–94, mostly immature birds), the most important variable explaining bearded vulture distribution was ibex biomass. During the settling phase (1995–2001), the presence of birds (mostly maturing subadults) correlated essentially with limestone substrates, while food abundance became secondary.
5. The selection of craggy limestone zones by maturing bearded vultures might reflect nesting sites that are well protected against adverse weather, as egg laying takes place in the winter. Limestone landscapes, in contrast to silicate substrates, also provide essential finely structured screes that are used for bone breaking and temporary food storage, particularly during chick rearing. Finally, limestone substrates provide the best thermal conditions for soaring.
6. *Synthesis and applications.* Extrapolated to the whole Alpine range, these findings might explain both the current distribution of the subadult/adult population and the absence of breeding records for bearded vultures around release sites in landscapes dominated by silicate substrates. As reintroduced bearded vultures tend to be philopatric, we suggest that population restoration would be more efficient if releases were concentrated within large limestone massifs. This case study of the bearded vulture illustrates the need for continual adaptive management in captive release programmes.

Key-words: Alps, ecological niche factor analysis (ENFA), geographic information system (GIS), *Gypaetus barbatus*, habitat selection, niche modelling, reintroduction, species conservation

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Introduction

As part of modern strategies to counter the risks of biodiversity loss, reintroduction schemes are becoming more and more common world-wide (Sarrazin & Barbault 1996; Carroll *et al.* 2003). Usually relying upon individuals stemming from captive stocks (Wedekind 2002), they aim at reinstalling wild populations of extinct species, especially those that have been directly (over-killing) or indirectly (habitat loss, predator or competitor introduction) extirpated by humans (O'Toole, Fielding & Haworth 2002; Richards & Short 2003; Ripple & Beschta 2003; Schaub, Pradel & Lebreton 2004). Alternatively, they aim to reinforce relict populations of critically endangered species (Hodder & Bullock 1997; Wanless *et al.* 2002). However, reintroduction programmes will only be effective if the ecological requirements of a species or local population are well understood. Species extirpated before the onset of modern ecology are of particular concern because knowledge of their functional position within a local ecosystem (i.e. their ecological niche) is often poorly documented, with information often scarce or anecdotal (Breitenmoser 1998). On the other hand, expanding populations of released species provide an opportunity to unravel species' ecological needs. This is particularly true if the species shows a high degree of dispersal, when it might be assumed that individuals will first settle in those areas that offer the most suitable conditions. The information drawn from first released individuals can thus serve to estimate species' preferences, thereby guiding subsequent releases within an ongoing reintroduction programme. Reintroduced individuals therefore offer an opportunity to identify species' requirements more easily than long-established populations. We illustrate this with a study of resource selection in a newly reintroduced population of bearded vultures *Gypaetus barbatus* Linnaeus 1758 in the Alps.

The bearded vulture, or lammergeier, is a large scavenging raptor that feeds primarily on bones. It was extirpated from the European Alps between the end of the 19th century and the beginning of the 20th century, with the date of extinction varying among populations (Arlettaz 1996; Mingozi & Estève 1997). A large-scale reintroduction programme, based on release to the wild of birds just prior to fledging that were born in captivity, was launched in 1986 in Austria (Frey 1992). This was followed by regular releases in three further Alpine countries: France from 1987 onwards, and Switzerland and Italy since 1991. Up to July 2003, a total of 121 individuals has been reintroduced into the

Alps (Frey 2002; see list in Robin *et al.* 2004). About 60–65% of the released birds are believed to have survived (Frey 2002; Zink 2002), although this figure may underestimate mortality because released birds are monitored only passively, principally through patterns of bleached feathers, a marking technique that enables individual recognition only until the first moult (i.e. until 2–3 years of age). Also, the limited number of marking combinations available, as well as the difficulty of reading markings accurately, particularly by inexperienced observers, has generated some confusion about sighting records (Zink 2002). Feather bleaching has nevertheless illustrated the dispersal potential of the species: individuals released as far away as central Austria (375 km), eastern Switzerland (250 km) and southern France (230 km) have subsequently been located in Valais in the Swiss Alps.

The first successful breeding event of the released population occurred in 1997 in Haute-Savoie, France (Heuret & Rouillon 1998). It was followed by 13 further chicks that have fledged between 1998 to 2003, and there were six breeding attempts in 2002 (three in France and three in Italy). However, no successful breeding has occurred in Austria and Switzerland, in spite of numerous observations of mature individuals in these countries. Several birds released in the Swiss National Park (the only Swiss release site) settled in nearby Italy. The absence of established breeding pairs is particularly striking for Austria, as birds were reintroduced there from the very beginning of the programme. At least one pair bond was established close to the release site in Rauris, Austria, some years after the beginning of the reintroduction effort, and a total of seven successive pair bonds was formed over the years (Zink 2002). The reasons for this lack of success remain largely poorly understood.

Although no releases occurred in the Alps of Valais (south-west Switzerland), they are close to the French release site in Haute-Savoie (30 km from the Swiss border). Bearded vultures were observed in the area soon after the first French releases in 1987 (Arlettaz 1996). A network of observers was formed in Valais in 1988, and the sightings checked meticulously for reliability before being recorded into a database. Although several individuals, including some adults, have attempted to settle in Valais, no pair has attempted to breed and the few pairs consist of subadult individuals. In the mid-1990s, we noticed that the distribution of bearded vultures in Valais was heterogeneous, with the species showing a strong preference for particular areas but avoiding other apparently suitable mountainous zones.

During the last decade, with the growing availability of digitalized spatial data, geographic information systems (GIS) have received growing interest from conservation biologists. These tools allow better understanding of the species–habitat links and underpin many spatial predictions in wildlife management (Augustin, Mugglestone & Buckland 1996; Guisan & Zimmermann 2000; Jaberg & Guisan 2001; Cabeza *et al.* 2004; Johnson, Seip & Boyce 2004; Rushton, Ormerod & Kerby 2004). By performing a GIS-based habitat analysis using the Valais sighting data set, we sought to identify which key environmental factors explained the distribution of bearded vultures. An extrapolation of these findings to other zones within the Alps could enable an understanding of why maturing and adult bearded vultures occupy and breed in some areas, while others remain uninhabited. Recommendations can then be made for improving the ongoing international reintroduction programme.

Data and methods

We analysed the relationships between two GIS data sets: the distribution of vulture sightings and a set of environmental descriptors. This allowed us to quantify and model bearded vulture's ecological requirements.

ENVIRONMENTAL DESCRIPTORS

The study area was the canton of Valais in the south-western Swiss Alps. It covers 5191 km² (about 2.7% of the overall area of the Alpine massif, which is 191 000 km² wide), modelled by a 100 × 100-m resolution raster map, i.e. 519 124 1-ha grid cells, overlaid on the hectometric Swiss coordinate system (plane projection). Four categories of environmental descriptors were included in the analysis: (i) topographical (continuous variables), comprising altitude, slope and exposition (or aspect); (ii) geological (presence–absence), comprising compact limestone, marl, gneiss, granite, rocky area, scree and water (rivers and lakes); (iii) anthropogenic (presence–absence), comprising buildings; and (iv) biological, comprising forest and meadows (presence–absence), ibex *Capra ibex* and chamois *Rupicapra rupicapra* (biomass), sheep (density) and distance to release site.

The actual environmental variables were derived from information maps to provide quantitative (a requirement of ecological niche factor analysis, ENFA; Hirzel *et al.* 2002) and integrative information. In fact, vulture behaviour and resource selection are probably not influenced by the quality of a single hectare but rather by characteristics of a wider area (which we assumed was circular). We envisaged three possible scales: (i) a sight-field scale of 500-m radius; (ii) a flight-search scale of 2000-m radius; and (iii) a long-range exploration scale (unlimited). The two first scales provided occurrence–frequency maps computed by means of a circular moving window, while the third provided a map of the distance to the closest occurrence. Accord-

ingly, each presence–absence descriptor generated three variables. We used the module CircAn of Biomapper (Hirzel, Hausser & Perrin 2002) and the module Distance of Idrisi32 (Eastman 1999) to perform these GIS operations.

The topographical descriptors were averaged by means of a 2000-m radius circular moving window and provided four variables: altitude, slope, northness (cosine of aspect) and eastness (sine of aspect); all were averaged on the moving window. We also computed the standard deviation of the altitude.

Wild ungulate biomass maps were built as follows. For the chamois, data were from a detailed census conducted in 1997–98 (Glenz *et al.* 2001) of the 24 cantonal gamekeeper districts and the federal and cantonal protected areas. For ibex, we had similar census data for every colony. In order to increase the spatial accuracy of the density estimations, we combined the census information to potential distribution maps of each species (Hausser 1995) to produce density maps (individuals ha⁻¹). These densities were finally multiplied by average sex- and age-dependent body mass (male, female and young: chamois, 30, 24 and 16 kg, respectively; ibex, 84, 33 and 22 kg, respectively; Game, Fishery & Wildlife Service, Valais, 1997, unpublished data) to give the biomass per grid cell (= kg ha⁻¹). Additionally, we computed a map of ibex observation density (kilometric resolution, database from the Centre Suisse de Cartographie de la Faune, 1999, unpublished data). We used our own data on sheep density (individuals ha⁻¹) for each summering pasture, and their spatial coordinates (Cantonal Veterinary Service, Valais, 1997, unpublished data). As information about the spatial extent of these pastures was lacking, we assumed a circular 2000-m radius shape for all of them. Where two such pastures were overlapping, we retained only the largest density. The distributions of all environmental descriptors were, as far as possible, rendered more symmetrical by the Box–Cox standardizing algorithm (Sokal & Rohlf 1981).

BEARDED VULTURE OBSERVATIONS

Throughout the Alps, ornithologists have been monitoring birds' movements since the beginning of the release programme. In Valais, a network of observers (Bearded Vulture Network Western Switzerland), in collaboration with the Cantonal Game, Fishery and Wildlife Service has collected and checked 1398 sightings, which stem from at least 29 different individual birds, from 1987 to 31 December 2001. Most identified birds (19 out of 29, *c.* 65%) originated from the release site in Haute-Savoie. Data recorded included date of observation, geographical location and, if known, the identity of marked birds.

Although the observation effort varied with the occurrence and effort of observers, we assumed that our data were representative of the actual geographical occupancy of the area by bearded vultures. Additionally, we controlled for any possible bias in observation

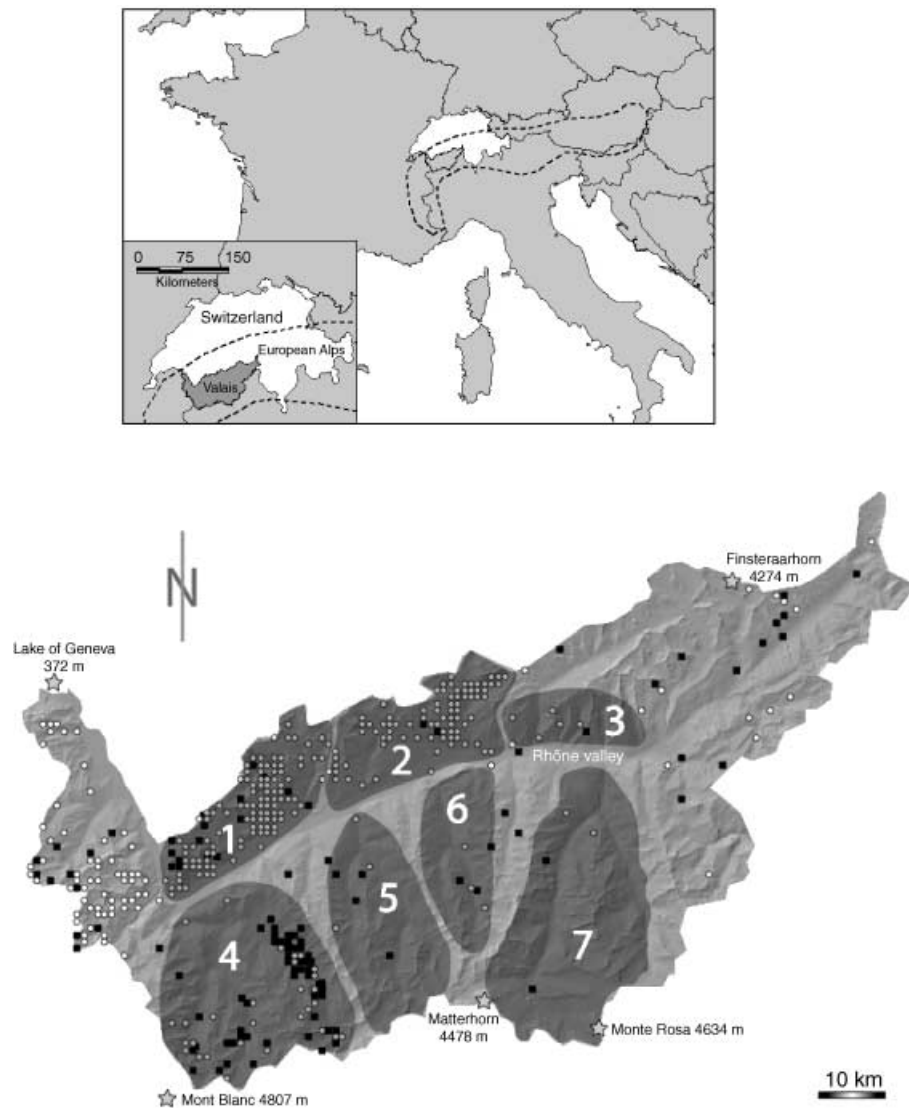


Fig. 1. Top: location of Valais in the European Alps and Switzerland. Bottom: hill-shade map of the study area (Valais, Switzerland) showing 1-km² squares with bearded vulture observations from 1987 to 1994 (black squares) and from 1995 to 2001 (white circles). The geographical subdivision of the study area is depicted by numbers (see Fig. 4).

clustering by subdividing the study area into major valley systems for which observation effort within a golden eagle *Aquila chrysaetos* monitoring programme was quantified (P. A. Oggier). Bearded vulture sightings were also recorded systematically in the same area by the same observer, and an index of frequency of observations per observation time unit and year (1990–2001) could be estimated for each zone separately. Both species have converging soaring habits and frequently use similar routes. This enabled us to assess whether clusters of bearded vulture sightings were observation effort-dependent or reflected actual habitat preferences by the species.

The colonization of Valais showed two distinct chronological phases: (i) a prospecting phase (1987–94), when immature (i.e. mostly 1–3 years old) individuals mainly visited the south-western parts of Valais, i.e. the valleys south of the main Rhône valley axis, at the periphery of the release site in France; (ii) a settling phase (1995–2001), when mostly maturing birds (sub-

adults; ≥ 3 years old) attempted to settle down in the north-west of Valais. In order to investigate this change of behaviour and its possible link to new patterns of habitat selection, the observation data were divided into two subsets (Fig. 1). The second data set included a marginal number of observations of immature birds, which rendered our spatial analysis conservative because an even greater contrast would have been found if those immatures could have been removed from this second-phase analysis.

In the survey, vulture sightings were recorded at a 1-km resolution. We built two presence 100-m resolution maps, hereafter observation maps, by assigning each record to the central hectare of the kilometric square where the bird had been seen.

HABITAT ANALYSIS

A variety of methods have been developed to model species' habitat and potential distribution (Guisan &

Zimmermann 2000; Rushton, Ormerod & Kerby 2004). The majority are based on presence–absence species' data sets. They make the intuitive assumption that the presence of a species is an indicator of suitable habitat and its absence an indicator of unsuitable habitat. However, there are many cases where these assumptions are not correct. In many cases, absence data are either unavailable (e.g. museum data, herbarium, atlas data) or unreliable (e.g. cryptic species, metapopulation following extinction–recolonization dynamics, invading species) (Hirzel, Helfer & Métral 2001; Peterson 2001; Hirzel *et al.* 2002; Peterson *et al.* 2002; Engler, Guisan & Rechsteiner 2004). In the case of the bearded vulture, absences were unreliable for two main reasons. (i) Being philopatric, this raptor is slowly spreading from its release site, therefore lack of sighting in some locations might be caused either by unsuitable conditions (true absence) or by the site being too far and yet unreached (false absence). (ii) This bird explores a wide area every day, making any systematic sampling of absences difficult. The first reason is particularly problematic as the case of a spreading species has been shown to fool a presence–absence-based method (generalized linear model; Hirzel, Helfer & Métral 2001). Therefore, we had to use a presence-only approach and we selected the ENFA (Hirzel *et al.* 2002) as it has been shown to be robust to spreading-species bias (Hirzel Helfer & Métral 2001); it has been applied to several studies based on presence-only data (Zaniewski, Lehmann & Overton 2002; Dettki, Lofstrand & Edenius 2003; Reutter *et al.* 2003; Thomas 2003; Brotons *et al.* 2004; Engler, Guisan & Rechsteiner 2004). A further advantage of the ENFA is that there is no descriptor selection, a sensitive process when stepwise procedures are involved. Instead, the ENFA computes a weight for all descriptors indicating their importance for the species' niche and their correlations.

ECOLOGICAL NICHE FACTOR ANALYSIS

The ecological niche of a species is potentially shaped by a large number of variables, with various levels of importance. Moreover, most of these variables exhibit some degree of correlation. ENFA extracts all relevant information from these variables while discarding their correlations and the background noise. It does so in a similar way to principal components analysis (PCA) by computing new, uncorrelated factors, a few of them summarizing most of the information. The main difference between PCA and ENFA is the nature of the data sets (here a data set is a population of vectors, the components of which are the values of the descriptors recorded at a grid cell). The PCA is computed on a single data set and its factors (or components) seek to find the directions that maximize the descriptor variances in the multidimensional environmental space. In contrast, the ENFA is based on two data sets: (i) the global set stores the descriptor values for all cells in the study area, and (ii) the species set stores these values for only

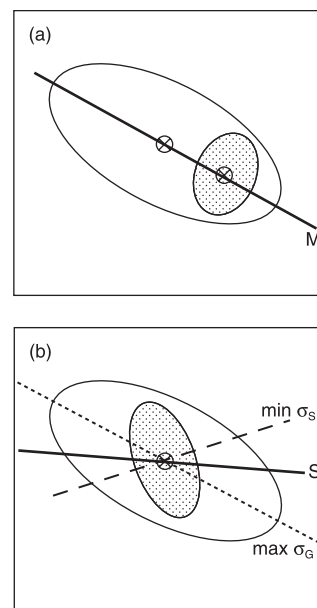


Fig. 2. Geometrical interpretation of marginality and specialization factors. The two-dimensional distribution of the global and species sets are symbolized by white and dotted ellipses, with a crossed-circle marking their centroids. The marginality factor (M) is the axis passing through both centroids. Once marginality has been extracted, both distributions have a common centroid and the specialization factor (S) is the axis maximizing the ratio of global variance σ_G to species variance σ_S ; it is intermediary between the axes of maximal global variance (dotted line) and minimum species variance (dashed line). See text for further details.

those cells where the species is present; it is therefore a subset of the global set. The ENFA factors result from the comparison between these two sets, and they are therefore directly interpretable. The first ENFA factor maximizes the absolute value of the marginality, defined as the standardized difference between the species mean and the global mean on all descriptors. It is geometrically figured by the line passing through the centroids of both the species and global sets (Fig. 2a). The marginality coefficients range from -1 to $+1$. Positive or negative values indicate a species' optimum higher (respectively lower) than the average conditions in the study area. Once the marginality factor has been extracted, the global and species sets centroids are coinciding. All the subsequent factors maximize the specialization, defined as the ratio of the global variance to the species variance. A specialization factor is geometrically figured by a line intermediary between the direction of maximum global breadth and the direction of minimum species breadth (Fig. 2b). Specialization coefficients range from -1 to $+1$, but only their absolute value is meaningful. A high value indicates a narrow niche breadth in comparison with the available conditions.

Finally, there are as many factors as descriptors. The first one explains all the marginality and some part of the specialization. The subsequent factors explain the remaining specialization in decreasing amounts.

Table 1. Environmental descriptors retained for the habitat analysis. Except when stated otherwise, they were derived from the GEOSTAT database (Swiss Federal Office of Statistics, Neuchâtel, Switzerland). EGV = ecogeographical variables

Variable category	Environmental descriptor	EGV code
Topographical	Average altitude in a 2000-m radius	ELEV
	Average slope in a 2000-m radius	SLOPE
	SD of altitude in a 2000-m radius	SDELEV
	Average northness in a 2000-m radius*	NORTH
	Average eastness in a 2000-m radius†	EAST
Geological	Frequency of limestone area in a 2000-m radius	CALC-2K
	Distance to limestone area	CALC-D
	Rock frequency in a 2000-m radius	ROCK-2K
	Rock frequency in a 500-m radius	ROCK-500
	Distance to granite area	GRANIT-D
	Scree frequency in a 2000-m radius	SCREE-2K
	Scree frequency in a 500-m radius	SCREE-500
	Distance to screes	SCREE-D
	Water frequency in a 2000-m radius	WATER-2K
	Water frequency in a 500-m radius	WATER-500
Anthropogenic	Building frequency in a 2000-m radius	BUILD-2K
Biological	Forest frequency in a 2000-m radius	FOREST-2K
	Forest frequency in a 500-m radius	FOREST-500
	Ibex biomass index‡	IBEX-BM
	Ibex frequency in a 2000-m radius‡	IBEX-2K
	Chamois biomass index‡	CHAM-BM
	Sheep density in a 2000-m radius‡	SHEEP-2K
	Distance to release site§	RELEASE-D

*Cosine of aspect.

†Sine of aspect.

‡Derived from Swiss Federal Game statistics, Bern, Switzerland.

§Computed in the GIS.

Usually, the most significant part of the information is gathered in a few of the first factors, thus reducing the problem complexity. The factors are given by their coefficients along the environmental descriptors and provide information about the species' marginality and specialization on each of them. Moreover, the global marginality and specialization coefficients integrate all these descriptor-specific scores, providing general clues about the species' niche. The global marginality ranges from 0 to 1 and indicates how far, all descriptors being accounted for, the species optimum is from the average conditions in the study area. The global specialization ranges from 1 to infinity; for ease of interpretation, the global tolerance coefficient, defined as the inverse of the specialization, is usually preferred as it ranges from 0 to 1. It is an indicator of the species' niche breadth. It must be noted though that these coefficients are relative to the study area and can only be used to compare species modelled with the same set of predictors. A detailed mathematical demonstration of the ENFA is beyond the scope of this paper and we refer the interested reader to our basic description (Hirzel *et al.* 2002).

The ENFA analysis was first applied to all the available environmental descriptors of the full set of observations (immatures and subadults pooled together); this was done in order to select the variables relevant for the bearded vulture distribution. Then, the ENFA was applied with the reduced descriptor set (listed in

Table 1) to both observation subsets. This provided two ecological niche models, one for the prospecting phase (1987–94) and one for the settling phase (1995–2001). All these analyses were made within the eco-GIS package Biomapper 2.1 (Hirzel *et al.* 2002).

HABITAT SUITABILITY MODELLING

The two models were then used to compute a habitat suitability map by means of the geometric mean algorithm (Hirzel & Arlettaz 2003). This algorithm works in the multidimensional environmental space defined by the most significant ecological niche factors computed by the ENFA. The species set defines a cloud of points in this environmental space, the density of which varies greatly and is assumed to be positively correlated with the suitability of any particular combination of descriptor values. This density is modelled for every hypervolume element (voxel) of this space by the geometric mean of its distances to all observation points; the higher the density of observations around a given voxel, the lower the mean distance. These distances are transformed into habitat suitability indices by delineating hypersurfaces (or envelopes) linking all voxels that have the same value (like the altitude isolines of a topographic map). An envelope suitability index is computed as the proportion of observation points outside it; for instance, the envelope 0.9 encloses 10% of the observations and leaves out 90% of them. These envelopes

are then transported to the classical geographical space to produce a habitat-suitability map. We chose to keep only the envelopes 0.5 and 0.9. The inner envelope (enclosing 50% of the observations) geographically defines a region we called core habitat. The geographical area located between the two envelopes (40% of observations) was termed marginal habitat. The area outside the external envelope (10% of observations) was considered unsuitable. See Hirzel & Arlettaz (2003) for further information about this algorithm.

MODEL EVALUATION

Observation points not used to calibrate the model were held on a validation set. Two indices could then be computed: (i) the absolute validation index (AVI), which is the proportion of validation points occurring in the predicted core habitat; and (ii) the contrast validation index (CVI), which is the AVI minus the AVI that would have been obtained with a hypothetical model that would predict core habitat for all cells of the study area. The latter index gives an indication of how well the model discriminates poor from good habitat. Both AVI and CVI were submitted to a cross-validation process (Sokal & Rohlf 1981; Manly 1991; Fielding & Bell 1997), allowing the computation of confidence intervals: the observation data set was partitioned into 100 subsets of which, alternately, 99 were used to calibrate the model (calibration set) and 1 to validate it (validation set).

Results

The first ENFA including all environmental variables and all the observations showed that some variables were not relevant to the bearded vulture distribution: all gneiss- and marl-related variables, 500- and 2000-m radius granite frequency, distance to water, distance to rock, 500-m radius frequency of human buildings and distance to them, all meadow-related variables, and distance to forest. The retained variables are listed in Table 1 and were used for all subsequent analyses.

PROSPECTING PHASE (1987–94)

For this period, 310 observations were analysed. The ENFA computed a global marginality coefficient of 0.72 and a global tolerance coefficient of 0.66, indicating that the vulture was living in conditions rather uncommon in the study area but that its niche breadth was rather wide. By comparing the ENFA eigenvalues with the MacArthur's broken-stick distribution (MacArthur 1960; Hirzel *et al.* 2002), the first five factors were kept as significant for the subsequent analyses, explaining 70% of the information (100% of the marginality and 41% of the specialization). The marginality factor explained little of the specialization (6%), meaning that the vulture niche breadth was not particularly narrow for the variables for which its optimum was the furthest from the average conditions.

A slightly negative marginality coefficient (Table 2, factor 1) for altitude indicated that, on average, the

Table 2. Correlation between ENFA factors and the environmental descriptors for the prospecting phase (1987–94). The percentages indicate the amount of specialization accounted for by the factor (moreover, factor 1 explains 100% of the marginality)

	Factor 1† (6%)	Factor 2‡ (18%)	Factor 3‡ (13%)	Factor 4‡ (8%)	Factor 5‡ (7%)
ELEV	–	*****	0	*	***
SLOPE	+++	*	**	*	0
SDELEV	+++	*	*	0	*
NORTH	--	*	*	**	*
EAST	–	*	0	0	*
CALC-2K	++	*	0	****	0
CALC-D	–	0	0	****	0
ROCK-2K	+	***	**	****	****
ROCK-500	+	*	**	**	**
GRANIT-D	0	0	0	****	0
SCREE-2K	++	*	*	**	**
SCREE-500	+	0	**	**	****
SCREE-D	--	0	0	0	****
WATER-2K	++	*	*	**	*
WATER-500	+	0	0	0	*
BUILD-2K	–	***	*****	**	***
FOREST-2K	+	0	*	0	****
FOREST-500	0	*	**	*	0
IBEX-BM	++	0	0	0	0
IBEX-2K	++++	0	0	0	*
CHAM-BM	+	0	0	*	0
SHEEP-2K	++	0	0	*	0
RELEASE-D	-----	*	*	*	0

†Marginality factor. The symbol + means that the vulture was found in locations with higher values than average. The symbol – means the reverse. The greater the number of symbols, the higher the correlation. 0 indicates a very weak correlation.

‡Specialization factor. The symbol * means the vulture was found occupying a narrower range of values than available. The greater the number of asterix, the narrower the range. 0 indicates a very low specialization.

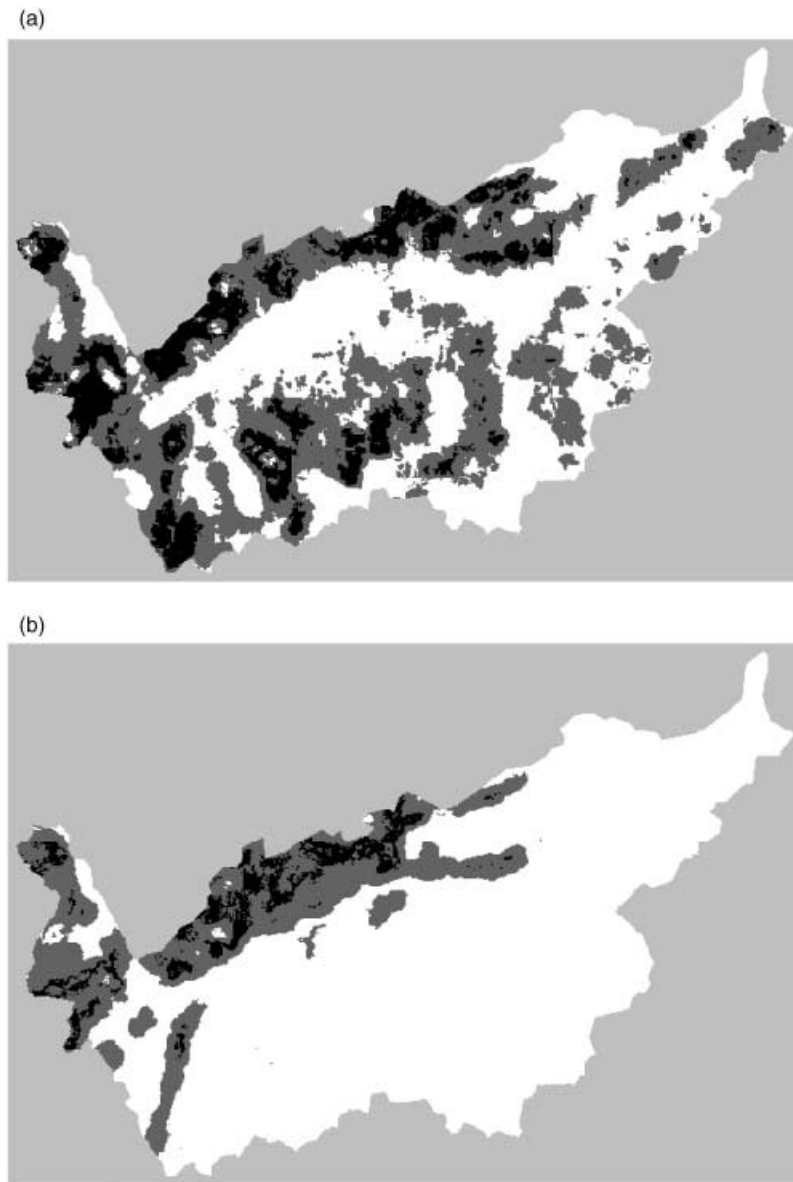


Fig. 3. Habitat suitability map computed for the (a) prospecting (1987–94) and (b) settling (1995–2001) phases showing the spatial distribution of the core (black), marginal (dark grey) and unsuitable habitats (white).

bearded vulture was found at lower altitude (2067 m) than the Valais average (2157 m). Furthermore, the high value of the first specialization factor (Table 2, factor 1) for this predictor indicated a narrow niche breadth, meaning that birds were rarely seen flying far from this altitude (SD = 503 m). Similar reasoning on the other coefficients showed that the favoured areas had steeper slopes than average (31° vs. 28°, respectively); their average northness (−0.11) and eastness (−0.02) and their relatively high marginality indicated a preference for slopes orientated towards the south or south-west. Nevertheless, the bearded vulture showed a very low level of specialization on these three variables. Other outstanding landscape-related features were specialization for rocky areas (mainly limestone and screes), relatively high frequency of water, avoidance of human settlements and some

specialization for areas with a slightly higher forest frequency than average (at the 2000-m radius scale). The highest marginality was related to ibex and sheep presence and proximity to the release site; however, the vultures were again very tolerant regarding these variables (all five specialization coefficients were null or very low).

Considering the sensitivity to different scale patterns, the vulture was almost always more marginal at the 2000-m than 500-m radius scale, or at distances greater than 2000 m; the specialization showed the same tendency. The cross-validation gave a mean AVI of 0.49 (SD = 0.13) and a mean CVI of 0.34 (SD = 0.13) (both values cannot be greater than 0.5). This means that, while the presence prediction power was very good, it could be due to a general overestimation of the habitat suitability (Fig. 3).

Table 3. Correlation between ENFA factors and the environmental descriptors for the settling phase (1995–2001). The percentages indicate the amount of specialization accounted for by the factor (moreover, factor 1 explains 100% of the marginality)

	Factor 1† (10%)	Factor 2‡ (16%)	Factor 3‡ (9%)	Factor 4‡ (9%)	Factor 5‡ (7%)	Factor 6‡ (6%)
ELEV	--	*****	*****	**	*****	***
SLOPE	+	**	0	***	****	*
SDELEV	++	***	*	*	***	*
NORTH	---	***	*	*	*	*
EAST	++	*	**	0	**	0
CALC-2K	+++++	*	*	*	*	**
CALC-D	-----	0	**	***	*	*****
ROCK-2K	+	*****	****	*****	***	*
ROCK-500	+	*	0	0	*	*
GRANIT-D	+	*	0	*	*	0
SCREE-2K	+	*	*	*	*	*
SCREE-500	0	**	0	*	*	**
SCREE-D	0	**	0	*	0	*****
WATER-2K	0	*	0	**	*	*
WATER-500	0	0	0	0	0	*
BUILD-2K	+	0	**	0	***	0
FOREST-2K	+	**	***	*****	*	**
FOREST-500	0	*	0	*	*	*
IBEX-BM	0	**	*	*	*	*****
IBEX-2K	++	0	*	*	0	*
CHAM-BM	+	0	0	0	0	*
SHEEP-2K	++	*	0	0	*	0
RELEASE-D	---	0	**	**	**	**

†Marginality factor. The symbol + means that the vulture was found in locations with higher value than average. The symbol – means the reverse. The greater the number of symbols, the higher the correlation. 0 indicates a very weak correlation.

‡Specialization factor. The symbol * means the vulture was found occupying a narrower range of values than available. The greater the number of asterix, the narrower the range. 0 indicates a very low specialization.

SETTLING PHASE (1995–2001)

More observations (1088) were available for this phase, but the global tolerance coefficient remained almost identical (0.65 vs. 0.66), whereas the global marginality coefficient was larger (0.84 vs. 0.72). By comparison of the eigenvalues with the MacArthur's broken-stick distribution (MacArthur 1960; Hirzel *et al.* 2002), the first six factors were significant and were used in the subsequent analyses, explaining 79% of the information (100% of the marginality and 58% of the specialization). The marginality factor explained slightly more of the specialization (10% vs. 6%).

In this phase, the situation was far more contrasted, with a few variables accounting for most of the marginality and specialization (Table 3). The most striking feature was the high marginality related to limestone areas: the bearded vulture tended to be seen in limestone environments (an average of 28% of limestone area in a 2000-m radius circle around observation points) or close to them (mean distance 468 m). There was some evidence of specialization on this variable, indicating a narrow niche breadth. The distance to release site was less marginal than for immatures, indicating that the mature birds had spread further. The average altitude was slightly lower than for immatures (mean = 1864 m, SD = 638 m), whereas the marginality for forest frequency was similar. The preference for southwards slopes was stronger among settling adults but with a tendency

towards south-eastern slopes. Ibex- and sheep-related variables lost their outstanding marginality, but vulture distribution was still biased towards them.

The cross-validation gave a mean AVI of 0.5 (SD = 0.23) and a mean CVI of 0.45 (SD = 0.23). The contrast value was greater than in immatures, confirming the fact that this map is obviously more accurate (Fig. 3).

DENSITY OF SIGHTINGS VS. OBSERVATION EFFORT

The frequency of bearded vulture sightings was not dependent on local observation effort (Fig. 4). In geographical subunits 1 and 2 (compare Fig. 4 with Fig. 1), the observation 'reward' was definitely biased towards bearded vultures, actually confirming a more dense presence of the raptor in the north-western Valais Alps.

Discussion

GENERALITIES

The ecological requirements of reintroduced bearded vultures colonizing Valais differed markedly between the prospecting (1987–94) and settling (1995–2001) phases. Bearded vultures were globally more selective during the settling phase than during the prospecting phase. Habitat suitability maps also had a better predictive

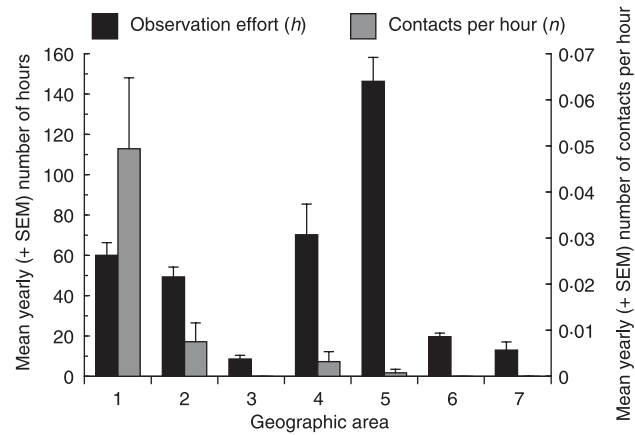


Fig. 4. Observation effort [mean (\pm SEM) number of hours per year] and reward [mean (\pm SEM) number of bearded vultures observed per hour \times year] in the various geographical subunits depicted in Fig. 1.

power in the second phase. It should be noted that bearded vulture distribution was more sensitive to environmental medium-extent variables (2000-m radius) than to small-extent variables (500-m radius). This is not surprising given that bearded vultures are potentially wide-ranging, and that our vulture observations were recorded at a 1-km resolution. Changes in ecological preferences did not result from changes in food abundance and distribution between the two phases: both ibex and chamois populations, as well as flocks of sheep, had similar densities and occupied similar ranges throughout the study.

BASIC PATTERNS OF HABITAT SELECTION

Our data show that bearded vultures tended to visit areas at lower altitude and with a higher forest cover than expected. Because of a wide altitudinal range in Valais (mountain ranges higher than 4000 m around the Rhône valley with a plain level of 372–680 m a.s.l.; Fig. 1) this altitudinal effect is not surprising as bearded vultures do not visit high peaks and glacier zones, where wild ungulate carcasses are absent. Additionally, bearded vultures also avoided the lowest altitudes, where human activity is high and where wild ungulates and sheep are rare; bearded vultures thus remain within a rather narrow altitudinal belt. The non-avoidance of forest at a regional scale might seem peculiar as bearded vultures tend to prefer open habitats in most of their range. In central Valais, however, because of the dry climate (Valais is the driest area within the Alps) and nature of the geological substrate, woodlands consist most often of small scattered trees and shrubs; they are thus readily accessible to bearded vultures. Moreover, in several areas such as game reserves, ungulates are numerous in forests in winter; this is also where lynx *Lynx lynx* hunt, providing additional carcasses. In central Valais, bearded vultures are often seen flying over sparse forests covering steep slopes, in search of carcass remains; they can land among scattered trees and shrub, or on rocky outcrops,

and walk several dozens of metres on forest ground to reach a carcass (R. Arlettaz, personal observations).

The preference for steeper slopes can be explained by the well-documented association of bearded vultures with cliffs, where they roost and nest, and because ungulates are more numerous in steep, remote areas, located further from human civilization.

Bearded vultures tended to be observed closer than expected to the release site in Haute-Savoie, from where most individuals that visit Valais originate (see the Introduction). Interestingly, this pattern did not differ strikingly between the prospecting and settling phases, indicating a philopatric tendency in the species.

During both prospecting and settling phases bearded vultures preferred areas with a higher density of ibex and sheep, although there was no link with the presence of chamois, another important source of food for bearded vultures in the Alps. However, chamois are abundant (*c.* 17 000 individuals) and widespread in Valais, where they inhabit a broader habitat spectrum and a wider altitudinal range than ibex (*c.* 5000 individuals); it is thus possible that a ‘chamois effect’ could not be detected because there was little variation in the abundance and distribution of this ungulate.

CHANGES IN HABITAT SELECTION PATTERNS: PROSPECTING VS. SETTLING PHASE

A change of slope orientation between the two phases can be explained by the frequent visits of birds during the first phase to a lateral (north–south orientated) valley south of the Rhône (Val de Bagnes), while subsequent sightings were mostly on the south-exposed slope of the main valley axis (ENE – SSW; Fig. 1).

A slight preference for areas not far from streams appeared during the prospecting phase but disappeared later. This is again probably because of an initial concentration of bearded vulture observations within major side valleys, whereas birds were then mostly seen in Central Valais, north of the Rhône, where lateral

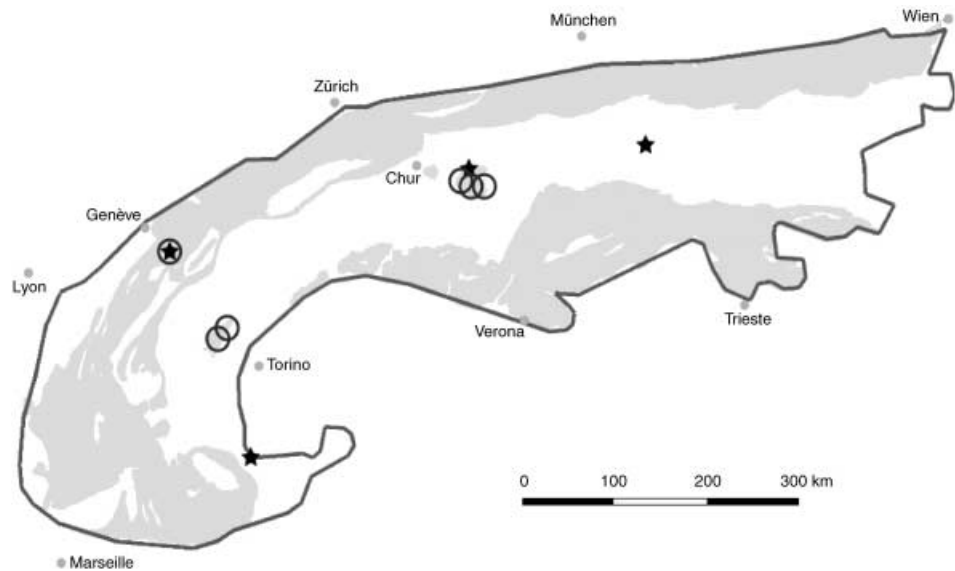


Fig. 5. Map of the European Alps (thick line) showing approximate limestone distribution (shaded), release sites (stars) and the first six breeding pairs (circles).

valleys are both much shorter and rare (Fig. 1) because of the limestone substrate.

Although the contribution of sheep and chamois did not differ between the two periods, ibex tended to be less influential in the second phase. This may be because roaming immature birds are mainly concerned with finding and tracking food resources, whereas subadults and adults have additional ecological requirements that are not uniquely trophic.

This interpretation makes sense when considering the geological variables that explain most of the habitat preferences during the second phase: limestone had a greater explanatory power than any other variable within the two models, pointing to a net selection for limestone zones. Such a preference was even clearer on comparison of the distribution map of records in Valais during the settling phase with a geological map: bearded vultures concentrated on the limestone zones (west and north-west Valais) but avoided metamorphic and silicate substrates (east and south of the canton; Fig. 1). We believe there are three, possibly not mutually exclusive, explanations for this selection pattern. First, the limestone areas in Valais belong tectonically to the Helvetic and external Alps, which are characterized by huge vertical cliffs rich in cavities and ledges (from a stratigraphic viewpoint, these cliffs belong essentially to late Jurassic and Cretaceous formations). Such recesses provide well-protected roosts and are excellent for eyries. This is important in the Alps where the bearded vulture reaches the northern border of its range: bearded vultures lay their eggs during winter, as early as February (Heuret & Rouillon 1998; Lücker 1998), which, at this latitude, can be marked by very adverse weather. In comparison, marl, metamorphic and crystalline (silicate) landscapes do not offer so many favourable breeding sites. A second hypothesis relates to the presence of suitable ossuaries.

These are places where bearded vultures break and temporarily store bones and bone fragments (Margalida & Bertran 2001). Usually screens with a fine-grained structure are favourite ossuaries, although rocky plates and outcrops may sometimes also be used. Accordingly, screens in limestone areas are abundant and widespread. Water is not easily retained in these rocks and so vegetation is scarce, giving a limestone landscape its typical arid appearance. Limestone screens also have a sharp-edged and fine structure, which enables bones to be broken into smaller fragments which are then more easily retrieved from among stones. This is not the case within silicate-stone areas, where screens are much scarcer and consist mainly of large blocks among which fragments would be difficult to retrieve; they also retain humidity, making them easily colonized by plants. Margalida & Bertran (2001) have demonstrated that ossuaries are of importance to the bearded vulture, especially during the breeding period when parents have to prepare delicate food items for the growing chick. Thirdly, limestone topography offers the best thermal conditions for this large raptor (with a *c.* 2.70 m wingspan), which seems to be of prime importance to bearded vultures (Haller 1983), particularly where they reach the northern border of their distribution range, as in Valais. Interestingly, north-western Valais, which offers the most suitable habitat according to our analysis, was the area where the last bearded vultures were reported prior to extermination in the 19th century (see map II in Fatio & Studer 1889).

IMPLICATIONS FOR REINTRODUCTION AND CONSERVATION

Our results show that food might be the principal driving force underlying habitat selection patterns in dispersing immature bearded vultures, whereas preparation

for reproduction might govern subsequent environmental preferences in subadults and adults. Interestingly, in the expert reports published during the preparation of the international bearded vulture programme (Müller & Buchli 1982), emphasis for the selection of suitable release areas in the Alps was put on wild ungulate density. Geology (although mentioned) was considered as a secondary factor, except possibly regarding the availability of cavities for placing captive birds to be released just before fledging.

Extrapolating from our own findings, we speculate that breeding bearded vultures recolonizing the Alps will initially occupy limestone areas (10–50% of rock coverage in a 2000-m radius), between 1500 and 2500 m altitude, that offer adequate cliffs rich in nesting sites and thermals as well as suitable bone-breaking screes. In our study area, we expect the areas delineated as core habitat (Fig. 3b) to be colonized first as they correspond to the most preferred conditions. However, as the population expands, bird density and competition are bound to increase, leading to less suitable habitats being exploited. The bearded vultures might then be expected to spread over the marginal habitat areas (Fig. 3b).

Already, data on settlement of the first breeding pairs of bearded vultures in the Alps up to 2002 seem to support our view (Fig. 5). In northern Italy, the three extant breeding pairs concentrate on a rather small, very arid limestone area. Geologically, this area is referred to as the Dolomitic Engadin Enclave, an isolated limestone area within much larger silicate units. In France as well, the three territorial breeding pairs have colonized wide limestone landscapes (National Parc of Vanoise, two pairs; Barge-Aravis range, one pair). In contrast, the silicate and flysch areas surrounding the Austrian release site, where reintroductions first took place as early as 1986, have failed to attract breeding pairs. This is also the case for the Swiss release site, located at the northern edge of the above-mentioned Italian Dolomitic Enclave.

Interestingly, five out of the six eyries occupied in 2002 were built on ledges or in niches in limestone cliffs. The only exception was one pair in the Vanoise National Park (Savoie, France), which used an old golden eagle *Aquila chrysaetos* eyrie in a silicate cliff. However, as this cliff is surrounded by limestone, this may suggest that the selection of limestone depends primarily on the availability of suitable ossuaries or thermals. The monitoring of the expanding adult bearded vulture population across the Alps will provide a further test of this hypothesis.

The observation that bearded vultures prefer limestone areas has potential implications for the release policy developed within the international reintroduction scheme. As bearded vultures exhibit some philopatric behaviour (Niebuhr 1993; Heuret & Rouillon 1998; this study), releases should optimally take place within major limestone Alpine massifs. Restricting reintroduction efforts to these landscapes would poten-

tially enhance survival rate, by increasing the attachment of birds to areas with the most suitable habitats, and by reducing the risks inevitably encountered by immatures during dispersal. However, it appears clear that the wide-ranging capacity of bearded vultures will ultimately enable them to find the most suitable zones on their own. On the other hand, our analysis also suggests that the failure to settle down and reproduce close to some release places might be due principally to suboptimal habitat quality around the selected reintroduction site.

It might seem unusual that, during the settling phase, the geological environment plays a more important role in habitat selection than the availability of ungulate carcasses, another essential component of territory selection. Yet, in this species the trophic function depends directly upon geology (screes for preparing food; Margalida & Bertran 2001) so that the two factors cannot be fully disentangled. As wild ungulates are now abundant and widespread in the Alps, in contrast with the situation in the past centuries until the extirpation of the species, they are unlikely to (as yet) represent a limiting factor for the breeding population, as we are probably at present far below the species' trophic carrying capacity. Density-dependent regulation is to be expected in the future, however. The monitoring of the spreading breeding population will tell us whether geological constraints will continue to play a major role in the future, or whether food requirements will further dictate spatial patterns of bearded vulture distribution within the Alpine range. In addition, it is important to stress that Valais is one of the driest areas of the Alps, which might also prove decisive for establishment.

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