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The increase in the Spanish population of Griffon Vulture *Gyps fulvus* during 1989–1999: effects of food and nest site availability

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Summary

Between 1989 and 1999, the Spanish population of Griffon Vulture *Gyps fulvus* increased from 8,064 to 22,455 breeding pairs. This increase was not linked to any clear density-dependent process of population control given that the population grew more steadily in the more densely occupied sectors. This growth was related to a small increase in the breeding range of the species supporting the strong effect of the availability of nesting sites in limiting the range of the species. Around 85% of the breeding pairs were restricted to limestone sectors where cliffs suitable for breeding colonies were more abundant. In these limestone sectors, changes in the number of breeding pairs were positively correlated to changes in livestock abundance during 1989–1999, supporting a functional relationship between food availability and vulture abundance. Any active destruction of livestock carcasses to prevent the spread of some epidemic livestock diseases (e.g. bovine spongiform encephalopathy, African swine fever, foot and mouth disease) will probably produce a concomitant reduction of the Spanish population of Griffon Vulture.

Resumen

Entre 1989 y 1999, la población española de Buitre Leonado aumentó de 8,064 a 22,455 parejas reproductoras. Este incremento no se asoció con ningún proceso de regulación poblacional dependiente de la densidad dado que la población creció más en aquellos sectores donde era más densa. Este incremento solo dio lugar a un pequeño aumento del área de distribución de la especie, lo que sugiere el efecto limitante de la disponibilidad de lugares de nidificación sobre la expansión de la especie. De hecho, el 85% de la población reproductora de buitres se concentró en las áreas calizas, donde abundan los cantiles adecuados para la instalación de las colonias. En estos sectores calizos, el aumento de la cabaña ganadera fue un buen predictor del aumento de la población de buitres. Esto parece apoyar la existencia de una relación causal entre la disponibilidad de carroñas y la abundancia de buitres. En consecuencia, una activa destrucción de las carroñas procedentes del ganado con el objeto de prevenir la expansión de diferentes enfermedades contagiosas (encefalopatía esponjiforme, peste porcina, brucelosis…) produciría una reducción numérica de los efectivos actuales de la especie.

Introduction

Spain holds more than 80% of the European population of Griffon Vultures *Gyps fulvus* (Hagemeijer and Blair 1997, Del Moral and Martí 2001). The numerical trends of this population are of paramount importance in determining the fate of this species at a global scale. During the 1980s and 1990s, this population has undergone a sharp increase. The 1979 national count estimated 3,249 breeding pairs (SEO 1981); the 1989 count, after improving the census cover, estimated 8,064 pairs (Arroyo *et al.* 1990); and the third count, carried out in 1999 with a similar census cover to 1989, estimated 22,455 breeding pairs (Del Moral and Martí 2001; Figure 1). Despite this spectacular increase, little information is available on the factors affecting these numerical trends (see Fernández *et al.* 1996 and Olea *et al.* 1999 for regional approaches), despite it being of paramount importance in predicting the fate of this population. For instance, there is some concern that, to prevent the spread of certain epidemic livestock diseases (e.g. bovine spongiform encephalopathy, African swine fever, foot and mouth disease), a rigorous observance of laws concerning the management of livestock carcasses would result in a sharp reduction of the main food source available to these scavengers (Del Moral and Martí 2001).

In this paper, we explore the growth of the Spanish population of Griffon Vulture during 1989–1999. Our main aim was to evaluate the role of some environmental factors affecting the spatio-temporal distribution of the increase in numbers of the species. We approached this from three related perspectives:

(a) We explored evidence of density-dependent regulation, i.e. whether vulture numbers in the more densely occupied sectors increased at lower rates than those in the less dense ones.

(b) We explored whether this increase was related to changes in food resources, in particular livestock availability (Griffon Vultures feed almost exclusively on livestock carcasses; e.g. Donázar 1993). This might indicate a functional relationship between food abundance and vulture numbers, although given the low rate of consumption of the available livestock biomass (De Juana and De Juana 1984, Arroyo *et al.* 1990, Donázar and Fernández 1990), food availability may only have a meagre effect, as it is just one of several factors affecting the growth of bird populations (Newton 1981, 1991).

(c) Finally, we examined the effect of nest site availability on the spatial patterning of this increase. Given that the Spanish population of Griffon Vulture depends largely on cliffs to nest, which in Spain are particularly abundant in limestone areas (SEO 1981, Donázar 1997), the contrasting availability of nestling places (e.g. limestone versus no-limestone sectors) may have shaped the population growth across the Spanish range affecting, for instance, the potential role of food availability on vulture numbers.

Methods

We studied the numerical change of the breeding population of Griffon Vultures by using the estimated number of breeding pairs per province during 1989 and 1999 (Arroyo *et al.* 1990, Del Moral and Martí 2001; Figure 1). From these data, we calculated the density of breeding pairs per province (pairs/100 km^2). We classified the provinces according to their distribution in limestone and

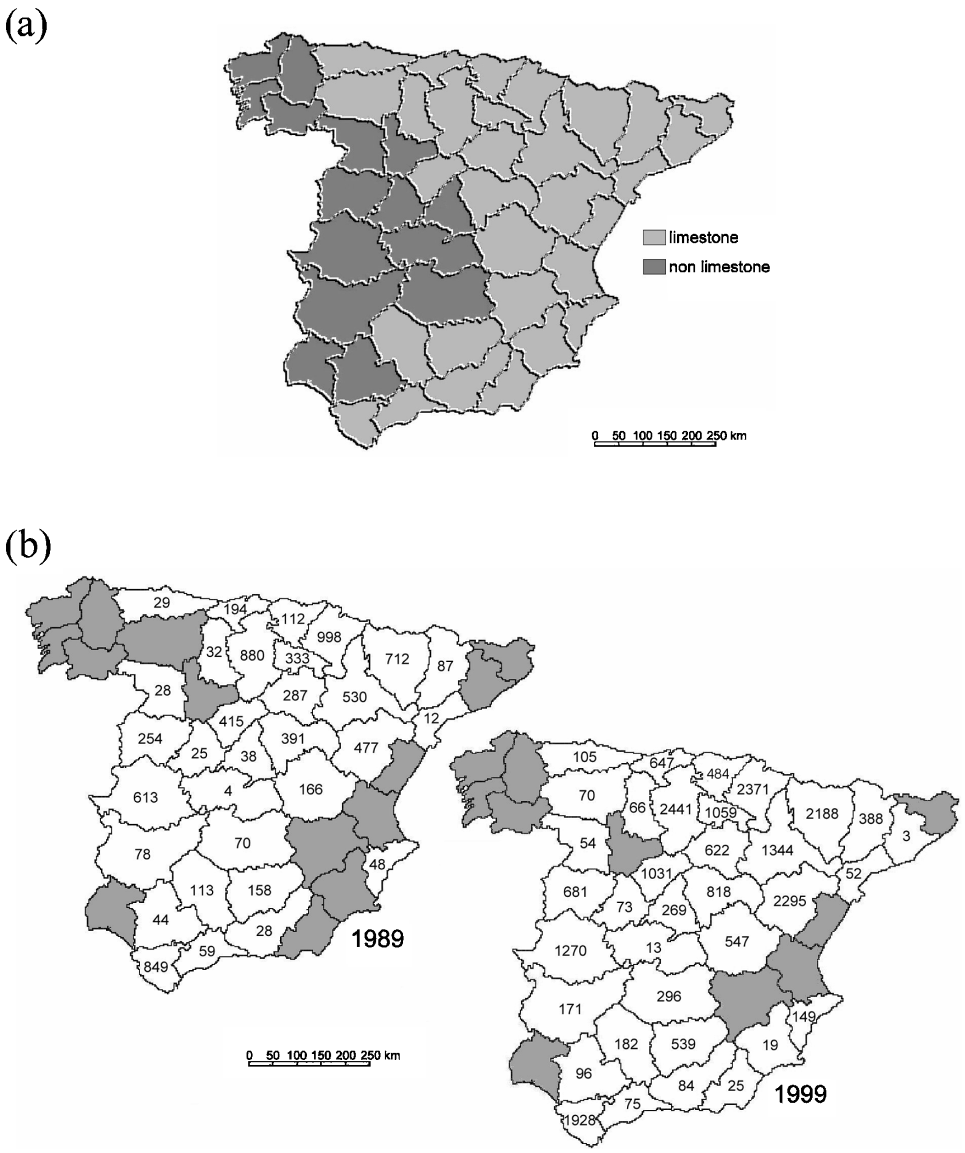

Figure 1. (a) Distribution of limestone and non-limestone provinces in Spain. (b) Distribution of the number of breeding pairs of Griffon Vulture during 1989 and 1999 (according to Arroyo *et al.* 1990 and Del Moral & Martí 2001).

non-limestone areas (Figure 1). We used the 1989 and 1999 provincial densities (D_{1i} and D_{2i}, where i refers to a given province) to make a regression analysis

$$D_{1i} = a + b \cdot D_{2i} \qquad [1]$$

If $b = 1$, we suspected a homogeneous increase of breeding pairs across the vulture range; if $b < 1$ we suspected density-dependent regulation (lower increase in provinces with the greater densities); and if $b > 1$ we suspected positive demographic feedback in the more densely populated provinces, with higher increases in those sectors where densities were greater (see Morris 1987, for a similar rationale).

We evaluated the availability of food resources for vultures by calculating the provincial livestock biomass available for vultures (we have assumed a constant rate of carrion production per province) by multiplying the number of each species by a standard body weight (550 kg for cow, 135 kg for pig, 55 kg for sheep, 65 kg for goat; data from Ministerio de Agricultura, Pesca y Alimentación 1989–1999, 1999, 2000). We evaluated the effects of 1989–1999 changes in food availability (R_{1i} and R_{2i}) on vulture densities (D_{1i} and D_{2i}) by using the habitat-matching rule (Pulliam and Caraco 1984, Fagen, 1988). This model states that all individuals will access a similar rate of resources wherever they are, so that the final patterning of densities will track resource distribution. As a consequence, inter-year changes in food availability in a set of i provinces will be tracked by densities according to the algorithm

$$\log (D_{2i}/D_{1i}) = a + b \cdot \log (R_{2i}/R_{1i}) \qquad [2]$$

where $b = 1$ if densities match efficiently the resources (all individuals have a similar rate of resources per capita) and $b < 1$ or $b > 1$ if density undermatches (e.g. inability of populations to exploit the richer sites) or overmatches (e.g. concentration in the best places) changes in resource availability (Kennedy and Gray 1993 for review). Lack of fitting in [2] illustrates the inability of the resource to predict abundance changes.

Results

Numerical regulation

The strong increase in the number of breeding birds was related to a very slight increase in the number of provinces occupied by the species (Figure 1). When comparing the densities of pairs between 1989 and 1999, we observed a sharper increase of vulture densities in the more densely occupied provinces ($b > 1$; Figure 2). This suggests a lack of density-dependent effects on the increase of the Spanish population of Griffon Vulture during the study period. However, the observed patterns did not change according to the availability of nesting places: both the limestone and non-limestone provinces showed a similar increase between 1989 and 1999, with denser areas showing higher rates of increase than less occupied ones (limestone provinces: $Y = 0.82 + 2.47^{**}$ X, $r = 0.97$ $P < 0.001$, $n = 26$; no n-limestone provinces: $Y = 0.50 + 2.10^{**}$ X, $r = 0.94$, $P < 0.001$, $n = 9$; ** $P < 0.05$ for signification from a slope of 1). This similar pattern of increase was related to the persistence of a similar ratio of breeding birds between areas, with 85% of the breeding pairs in limestone areas and 15% in non-limestone ones (Table 1).

Tracking of livestock biomass

Livestock biomass increased in the 1989–1999 period (Table 1), particularly from 1995 forwards (Figure 3). However, provincial changes in livestock biomass in

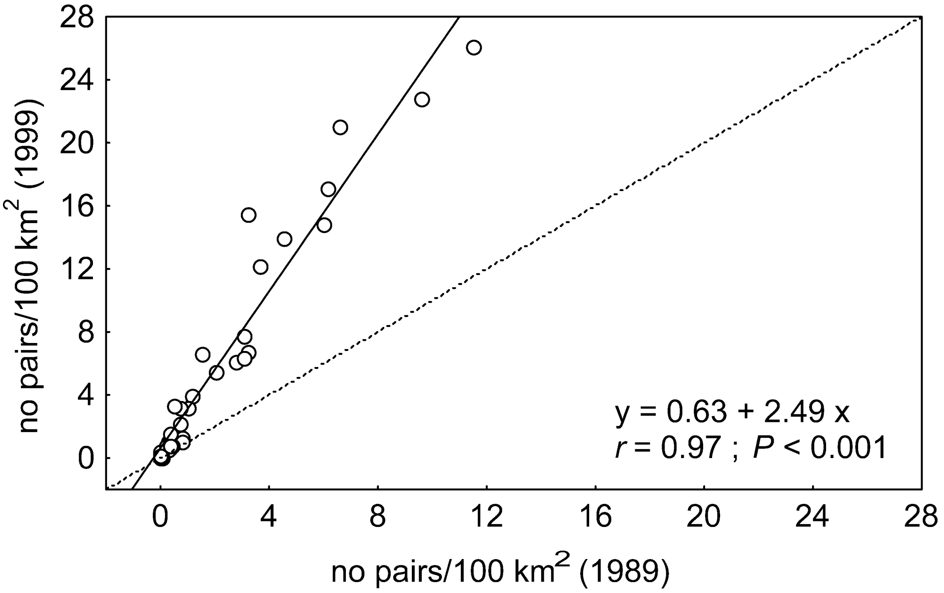

Figure 2. Relationship between the density of breeding pairs of Griffon Vulture in Spain per province in 1989 and 1999. Dotted line shows the hypothetical situation in which densities were identical between years. The regression coefficient significantly differs from 1 ($P < 0.001$).

Table 1. Distribution of the number of breeding pairs of Griffon Vulture, livestock biomass and the biomass/breeding pair ratio, in Spain and in limestone and non-limestone provinces during 1989 and 1999

	1989	1999
Total Spain		
Vulture population (no. pairs)	8,064	22,455
Livestock biomass (tm)	5,390,162	6,442,784
Biomass/pair ratio	668.43	286.92
Limestone provinces		
Vulture population (no. pairs)	6,895	19,532
Livestock biomass (tm)	3,595,175	4,416,703
Biomass/pair ratio	521.42	226.13
Non-limestone provinces		
Vulture population (no. pairs)	1,169	2,923
Livestock biomass (tm)	1,794,987	2,026,081
Biomass/pair ratio	1535.49	693.15

this period were not correlated with changes in vulture density across the Spanish range ($Y = 0.45 + 0.18X$, $r = 0.14$, n.s. $n = 31$). This result suggests, at first, no relationship between food availability and vulture numbers. However, this pattern seemed to be strongly affected by nest site availability: whilst changes in vulture density in non-limestone provinces did not reflect changes in livestock biomass ($Y = 0.47 - 0.40$ X, $r = -0.33$, n.s. $n = 9$), changes in limestone provinces did reflect changes in livestock biomass (Fig. 4). This suggested food resources

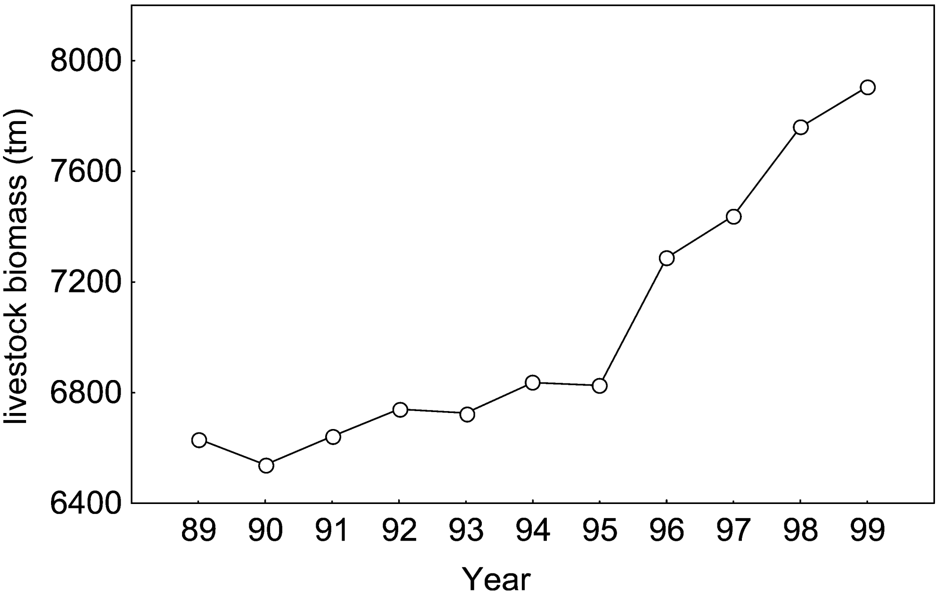

Figure 3. Trends of livestock biomass in Spain during the 1989–1999 period (Ministerio de Agricultura, Pesca y Alimentación 1989–1999, 1999, 2000).

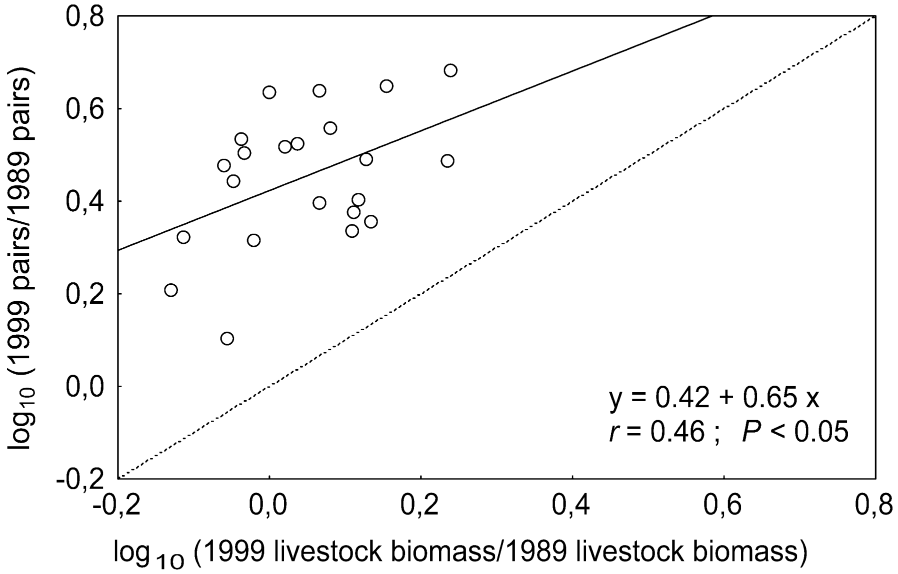

Figure 4. Relationship between changes in the number of Griffon Vulture pairs and changes in livestock biomass per province between 1989 and 1999. The regression coefficient does not differ significantly from 1. Dotted line as in Figure 2.

played a major role in influencing the Spanish population of Griffon Vulture (Table 1). The slope of the relationship between changes in vulture density and food availability in limestone provinces [2] was under 1 but did not differ statistically from unity (Figure 4). This supports the view that the population increase in limestone areas matched quite closely the evolution of food resources. It is interesting to note that the relative availability of food resources per breeding pair decreased in 1999 to a half of the 1989 level, being particularly sharp in limestone provinces (Table 1).

Discussion

Results in this study suggest at first that, despite the breeding population of the Spanish Griffon Vulture population increasing three fold between 1989 and 1999, there was no density-dependent process of numerical regulation since the population grew more steadily in the more densely occupied provinces (Figure 2). This large-scale pattern does not exclude, however, the onset of some local regulatory processes in the more densely occupied provinces, where decreased breeding success has already been observed (see e.g. Fernández *et al.* 1996). These could be related, for instance, to a decrease in available food resources per breeding pair during the last decade (Table 1), which in some areas could be a limiting factor for population growth. It is important to note that the absence of regulatory processes could have produced higher scores of the b slope [1] than observed in our results (Figure 3).

A second issue refers to the very small increase in the range of the species despite the sharp growth of the population, since only four provinces located outside the 1989 range were occupied in 1999 (Figure 1). As a similar pattern was already observed when comparing the distribution of vulture colonies between 1979 and 1989 (Arroyo *et al.* 1990), it can be concluded that the sharp increase in the Griffon Vulture population in Spain during the last 20 years has been associated with a meagre expansion of the breeding range from limestone to non-limestone provinces (Figure 1). As populations usually increase their range as their numbers grow (Gaston 1994), these spatial constraints can be related to the scarcity of suitable nestling areas outside the traditional limestone range of Spanish Griffon Vultures.

The unbridled growth of a population inside a restricted range can only occur when it is not severely limited by resources. According to this paper, the increase in vulture numbers in limestone areas was related to the increase in livestock biomass, a relationship that strongly supports a functional role of food availability. As the bulk of the Spanish vulture population occurs in these limestone sectors (Table 1), this tracking of food resources seems to be a key process in the observed population increase. The efficient spatio-temporal tracking of resources underlying this trend can be explained because vultures are able to track food resources across traditional and new feeding grounds by establishing breeding colonies near highly productive spots (e.g. mountains and pasturelands; Donázar 1993). This ability for tracking food in areas where nesting places are abundant is reinforced by the ability of individuals to move long distances from breeding colonies in the search for food (*c.* 50–70 km; Donázar 1993 for review).

Contrastingly, the scarcity of suitable nesting sites in non-limestone provinces prevents an efficient spatial tracking of livestock biomass changes. This could explain the relatively high availability of food resources per breeding pair (Table 1), a feature that does not necessarily mean that colonies in non-limestone areas will face higher availability of food resources than colonies in limestone areas. Breeding individuals of these colonies will patrol the surrounding areas in the search for food but will be unable to access far regions where available carcasses will be under-used or used by non-breeding floaters. It is important to note that the population increase in non-limestone sectors was similar to that observed in limestone areas (results from algorithm [1] and Table 1), a pattern that suggests a similar response of colonies to increasing availability of food resources. Thus, despite the inability of vulture populations to track spatial changes in food availability across the large non-limestone sectors, extant breeding colonies reacted to increasing food in the surrounding areas in a similar way to populations in limestone provinces.

These results support the hypothesis that livestock increases in Spain during the 1989–1999 decade were followed by a concomitant increase in vulture populations. It is thus logical to assume that, despite the Spanish vulture population apparently consumes only a small proportion of the available livestock biomass (around 0.5%; see De Juana and De Juana 1984, Arroyo *et al.* 1990), food availability is a major factor regulating the population. From this it follows that any decrease in food availability by active destruction of livestock carcasses accessible to vultures could produce a reduction of the Spanish population of the species. The strength of this decrease would depend, however, on the intensity of carcass removal, something difficult to accomplish in many large, inhabited areas where livestock and vultures occur. It will also be affected by our ability to use traditional feeders (*muladares*) or some new ad hoc feeding places as management tools in conserving vulture populations under safe health conditions (Donázar 1992).

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