

# Winners and losers in human-made habitats: interspecific competition outcomes in two Neotropical vultures

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## Keywords

Argentina; biotic homogenization; *Coragyps atratus*; interspecific competition; social foraging behaviour; *Vultur gryphus*.

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## Abstract

Understanding the factors underlying species coexistence is a major focus in community ecology. When dealing with competition between native and exotic species, the competitive exclusion of the 'weaker' species can have consequences for biodiversity conservation. We examined interspecific interactions during foraging between black vultures *Coragyps atratus* and Andean condors *Vultur gryphus* in Southern Argentina. Previous studies suggest facilitatory interactions between them. However, in most parts of their distribution ranges, these species did not coexist until recently, when black vultures expanded their geographic range following human development. Thus, facilitatory processes or segregation patterns could not be fine-tuned enough to allow their coexistence. Our hypothesis is that black vultures and Andean condors compete for food resources, and that this competitive scenario can change depending on local species abundances and habitat humanization. We experimentally placed sheep carcasses in two habitats differing in degrees of humanization to study the foraging patterns in these species. Both species exploited carcasses with similar temporal patterns. However, the first to arrive and the dominant species were different in both habitats, according to their abundances. Although black vultures do not completely prevent the arrival of Andean condors to carcasses, they represent serious obstacles for feeding. Thus, while dominance hierarchy at carcasses could be related to body size, carcass consumption was determined by species abundance. Our results support the hypothesis that the expansion of a 'winning' species may trigger interspecific competition with other 'loser' species, with negative responses towards human activities when they became abundant. Although the results are not conclusive, invasion and extinction processes could be occurring and they can have serious consequences for the diversity (i.e. richness and evenness) of the New World scavenger guilds.

## Introduction

Interspecific competition has been recognized as an important factor in shaping animal communities. In this regard, one of the most interesting questions is whether interspecific competition causes the exclusion of one species or results in their co-existence (Sommer & Worm, 2002). Theoretical and experimental studies on interspecific competition have concluded that a heterogeneous environment and an evolutionary trade-off between the abilities of the coexisting species to exploit different parts of an environment are essential for coexistence (e.g. Brown, Kotler & Mitchell, 1994; Wauters *et al.*, 2002; Carrete *et al.*, 2005). However, when an expanding species occupies the range of an ecologically

similar species that has evolved in its absence, the lack of niche differentiation may result in the competitive exclusion of the 'weaker', or less competitive, species.

Many examples exist of non-native species causing extinction or endangerments of native wildlife through interspecific competition (e.g. Griffis & Jaeger, 1998; Wauters *et al.*, 2002; Smith, 2005). However, direct anthropogenic introductions are not the only mechanism favouring the spread of species into new environments in which they are not native. Human activities cause many types of alterations in natural landscapes that can be exploited by certain alien species with positive responses towards these transformations (McKinney & Lockwood, 1999). Perhaps because these invasions may seem more 'natural', it is difficult to

recognize their ecological implications and they have been less studied as potential components of biodiversity change (Valéry *et al.*, 2009). However, the expansion of cosmopolitan, usually non-native but sometimes native species (referred to as 'winning species'; McKinney & Lockwood, 1999; Valéry *et al.*, 2009), and the contraction of rare, often endemic, native species (referred to as 'losing species'; McKinney & Lockwood, 1999) through the biotic homogenization process can be considered an unprecedented form of global change (Ricciardi, 2007) and one of the most important forms of biological impoverishment world wide (Olden *et al.*, 2004).

The black vulture *Coragyps atratus* can be considered an example of a winning species positively responding to human transformations (Carrete *et al.*, 2009). Although detailed studies on its large-scale geographic expansion are lacking, the scarce information available shows how the species, once limited to highly productive tropical habitats, has progressively advanced until its current occupation of broad regions of North and nearly all of South America (Darwin, 1839; Houston, 1985, 1988; Tonni & Noriega, 1988; del Hoyo, Elliot & Sargatal, 1994; Buckley, 1997; Schlee, 2000; BirdLife International, 2008a). The use of food resources associated with human development (rubbish dumps, cattle and road kills; del Hoyo *et al.*, 1994) seems to be the key factor that has made this expansion possible. The species now shares its range with all the other Cathartid vultures constituting a homogenizing factor *per se* (i.e. through the invasion pathway; Olden & Poff, 2003) of the scavenger guilds of the New World. Of greater concern is whether this species is competing for resources with others, in which case the outcome of the competition process may be that this invasion is associated with the extinction or the rarefaction of another, less competitive species (i.e. invasion and extinction pathway; Olden & Poff, 2003).

Here, we examined the importance of interspecific interactions during foraging between black vultures and Andean condors *Vultur gryphus*, one of the scavengers currently sharing their distribution range with the black vulture, and of utmost conservation concern (BirdLife International, 2008a,b). Previous studies suggest that larger Andean condors dominate smaller black vultures when feeding at carcasses, the latter species benefitting from facilitatory processes such as the opening and dismembering of large carcasses by Andean condors (see Wallace & Temple, 1987). However, in most parts of their distribution ranges, and specifically in the Southern Cone (i.e. Argentina and Chile), these species did not coexist until recently (<100 years; Darwin, 1839; Houston, 1985; Tonni & Noriega, 1988), when black vultures expanded their geographic range following human development and associated resources (del Hoyo *et al.*, 1994). Thus, facilitatory processes or segregation patterns could not be fine-tuned enough to allow their coexistence.

Our primary hypothesis is that black vultures and Andean condors compete for food resources instead of showing interspecific facilitatory relationships, which might trigger

conservation consequences for the scavenger guild. The fossil record (Tonni & Noriega, 1988) and some observational sources (Darwin, 1839; Houston, 1985, 1988; del Hoyo *et al.*, 1994; Schlee, 2000; BirdLife International, 2008a) support the idea that the two species have only interacted in the Southern Cone for a few decades, and so they lack a joint evolutionary history that would have adjusted competitive interactions (Rice & Pfennig, 2008). Although Andean condors should remain dominant over black vultures because of their much larger size, the extreme sociability and aggressiveness of the latter species when feeding at carcasses can presuppose a dominance advantage, mainly in those areas in which Andean condors are scarce (i.e. in humanized habitats; Donázar *et al.*, 1999; Speziale, Lambertucci & Olsson, 2008; Carrete *et al.*, 2009). This can make the competitive scenario between both species more dynamic and changeable than expected previously, and largely dependent on the local abundance of both competitors (Mönkkönen, Forsman & Thomson, 2004). Moreover, related to sexual size dimorphism and habitat-use patterns (females are smaller and use plains habitats more frequently than males; Donázar *et al.*, 1999), female Andean condors can be more affected by these interspecific interactions than males. Our first prediction is that the abundance of each species at carcasses will vary between habitats, with Andean condors being more abundant at carcasses located in mountains and black vultures being more abundant at carcasses located in plains, where human transformation is more prevalent. Second, we predict that both the probability of arrival of Andean condors at carcasses and the numbers of them feeding will be negatively affected by the abundance of black vultures at these points. Moreover, their co-occurrence rates at carcasses will be lower than expected in random (i.e. no interspecific interactions) or in facilitatory (i.e. a species makes access to food easier to others) scenarios. In all cases, these interspecific relationships will be more marked for female Andean condors than for males.

## Materials and methods

### Study species

Black vultures (1.1–1.9 kg) and Andean condors (female: 8–11 kg, male: 11–15 kg) currently share their ranges across South America, with Andean condors occupying principally natural open grassland and Andean regions up to 5000 m and black vultures distributed across human-transformed landscapes, being abundant around towns (del Hoyo *et al.*, 1994). Moreover, both species show clear imbalances in their population numbers and conservation status. Andean condors were once widely distributed along the Cordilleran range from Venezuela to Tierra del Fuego. Currently, the species is threatened mostly in the northern parts of its range, but is still relatively abundant in the south (BirdLife International, 2008b; Lambertucci, Jácome & Trejo, 2008). Conversely, black vultures have a large global population size, and the species is evaluated as of Least Concern (BirdLife International, 2008a).

## Study area and data collection

The study was conducted in Western Patagonia (Argentina), in an *c.* 7000 km<sup>2</sup> area of the Cordillera limited in the north by the city of Junín de los Andes (Neuquén province, 39°57'S–71°05'W) and in the southeast by the city of Bariloche (Río Negro province, 41°09'S–71°17'W). The climate is cold and dry, with a pronounced gradient of rainfall from 800 mm average annually in the mountains (1600 m a.s.l.) to 300 mm on the eastern steppes (600 m a.s.l.). The region belongs to the Patagonian phytogeographic province in the Western District (Cabrera, 1976).

We distinguished two main habitat types in the study area, that is mountains and plains, based on their degree of humanization and, therefore, suitability for and abundances of both species. In the mountains (up to 3600 m a.s.l.), there are many Andean condor roosts and breeding areas (Donazar *et al.*, 1999; Lambertucci *et al.*, 2008), and human disturbance is very low, with some isolated human settlements and a few unpaved roads. In contrast, Andean condors are less abundant in plains (between 500 and 900 m a.s.l.), which are more populated (Junín de los Andes: 15 000 inhabitants, and Bariloche: 130 000 inhabitants) and have more infrastructure (i.e. paved roads) than mountains. Consequently, plains could be considered as a suboptimal habitat for Andean condors, while mountains, where the species is more abundant, can be considered as high-quality habitats. Black vultures, however, are more abundant in plains, because they concentrate in high numbers (up to 300 individuals) in the vicinity of towns and refuse dumps (Donazar *et al.*, 1993, 1999).

We experimentally placed 32 sheep *Ovis aries* carcasses in the two contrasting habitats (21 carcasses in mountains and 11 carcasses in plains), during November–December 1991 and 1992, January–February 1995 and October–December 2006. As four carcasses were not used by the study species, our sample size for analysis was reduced to 28 carcasses. Although scavengers in Patagonia originally depended on carcasses of native camelids, mainly guanaco *Lama guanicoe*, they are nowadays heavily reliant on carcasses of domestic ungulates, mainly sheep (Lambertucci *et al.*, 2009). Thus, we can be confident that our observations have no biases associated with the use of this resource during the experiment.

Each carcass was monitored from the moment at which it was placed in the field (*c.* 2 h after dawn) until its complete consumption. Observations were made by two observers from a hidden location or a vehicle at a minimum distance of 300 m to avoid interference with bird behaviour. We systematically recorded information on the first species to arrive at a carcass and the abundance of each species every 10 min. Although this last point may suggest that the same observation is noted several times, the activity at carcasses was very dynamic, with continuous changes in the number of individuals due to the constant arrival and departure of birds (authors unpubl. data). Because Andean condors show strong sexual size differences, with males dominating females at carcasses during foraging (Donazar *et al.*, 1999), we

recorded the sex of each individual (see del Hoyo *et al.*, 1994 for sexual differences).

## Statistical analysis

We considered that similar patterns of both species in the abundance of individuals using carcasses through time could be indicative of a scenario prone to interspecific interactions. Otherwise, interspecific competition would be precluded through differences in their temporal patterns of carcass use. Thus, we first explored the relationship between the abundance of each species and time through generalized linear mixed models (GLMM; link function: logarithmic, error distribution: Poisson), including 'carcasses' and 'years' as random terms to avoid pseudo-replication and inter-annual variability.

After testing whether both species showed a similar temporal trend in carcass exploitation, we used information gathered during the 10-min intervals to evaluate the actual degree of co-occurrence between them. We generated, through 1000 randomizations, the expected distributions of co-occurrences of both species considering mountains and plains separately to compare our observations. We performed three different sets of simulations. First, we randomly shuffled all observations of Andean condors (considering females and males separately) and vultures. Subsequently, we alternatively kept fixed the observations of one species while the observations of the other were randomized. Under a scenario of interspecific competition and exclusion, the number of co-occurrences between species should be lower than expected at random. Conversely, if both species are more frequently associated than expected at random, potential facilitatory processes (i.e. Andean condors facilitate carcass consumption by black vultures by opening them or black vultures facilitate carcass location by Andean condors because of their larger numbers; Wallace & Temple, 1987) should not be discarded.

We tested differences between mountains and plains in the species that first arrived to carcasses through GLM. Then, using GLMM, we assessed the effects of the number of heterospecifics on the probability of arriving at a carcass (link function: logistic, error distribution: binomial) and on the number of birds feeding on them (link function: logarithmic, error distribution: Poisson). Habitat differences were tested including mountains and plains as levels within a fixed factor. We included *carcass* and *year* as random factors to control for variability among years, carcasses and carcass locations, and to avoid non-independence of the data.

## Results

### Carcass use and co-occurrence of competitors

Sheep carcasses were available in the field for around 28 h, and there was no significant difference in their persistence time according to habitat type (mountains: 30 ± 26 h,

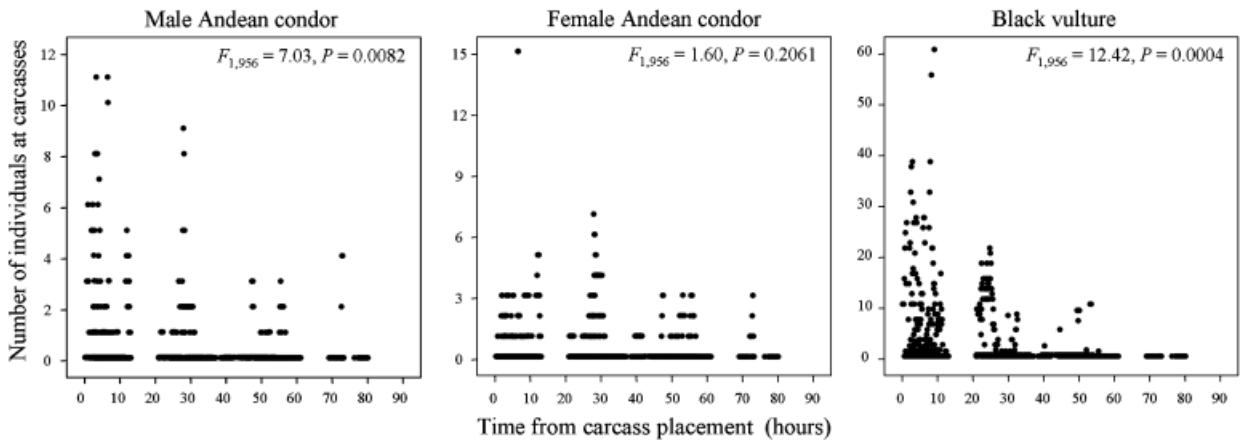
$n = 18$ , plains:  $23 \pm 18$  h,  $n = 11$ , Mann–Whitney  $U$ -test:  $P = 0.653$ ). Although there is a significant variability among carcasses ( $P < 0.005$ ), male Andean condors and black vultures arrived in larger numbers during the first hours after carcass detection (Fig. 1). Moreover, the negative relationship between species abundances and time also showed that they display a common temporal pattern of resource use, which may favour a scenario for interspecific interactions in sympatric areas. The pattern of female Andean condors, however, showed no significant relationship with time.

Records taken at 10-min intervals revealed that the number of co-occurrences observed between both species was always significantly lower than that expected at random

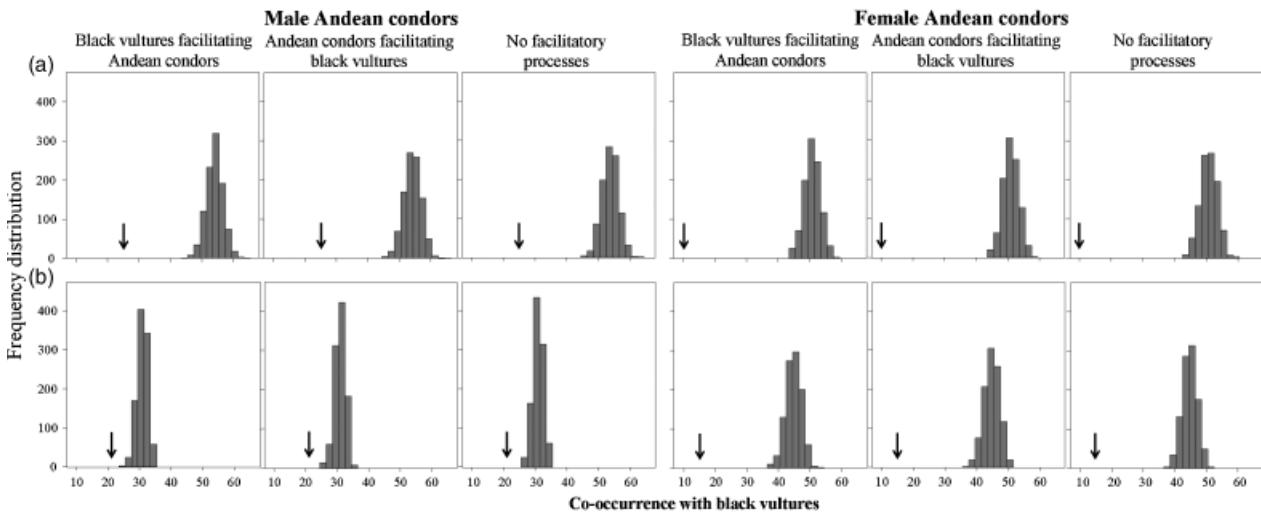
(all  $P < 0.001$ , Fig. 2). This result, equal in the two habitats considered, lends stronger support to a scenario of interspecific competition than to a scenario of food facilitation.

**Interspecific differences in carcass use between habitats**

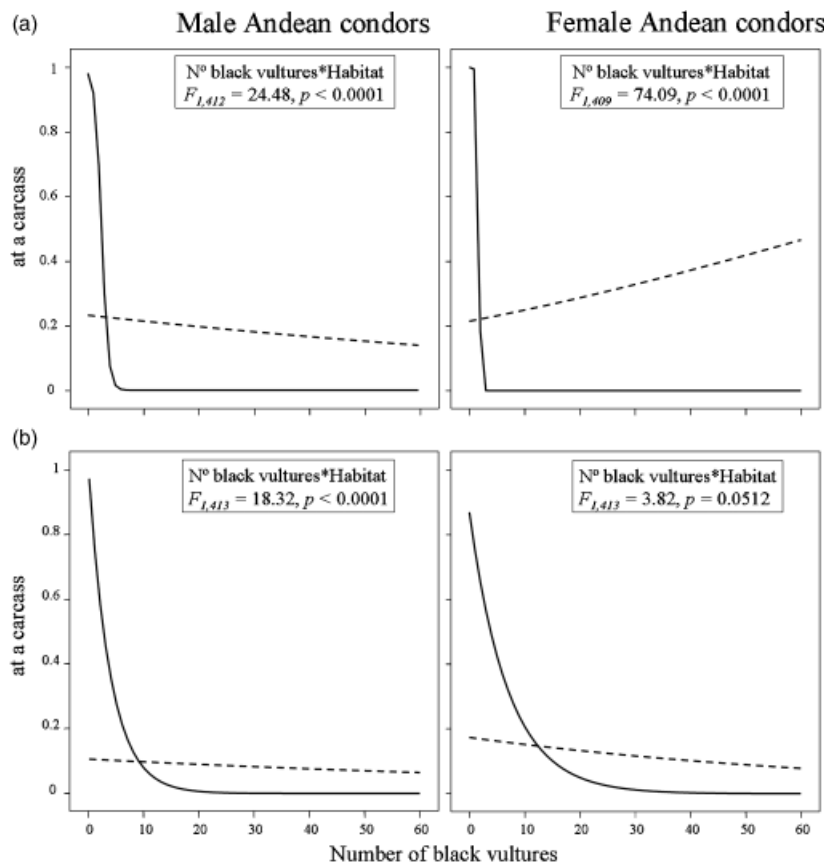
The first species to arrive at carcasses was not the same in the two habitats considered ( $\chi^2 = 5.45$ ,  $P = 0.0195$ , d.f. = 1). Andean condors arrived first to 76% of carcasses placed in mountains, while black vultures arrived first to 72% of carcasses placed in plains. These differences were in accordance with differences in the number of individuals of each species recorded at carcasses every 10 min, with



**Figure 1** Abundance of male and female Andean condors *Vultur gryphus* and black vultures *Coragyps atratus* at carcasses through time. Note that plots are raw data while analyses are controlling for carcass identity.



**Figure 2** Number of co-occurrences of male and female Andean condors *Vultur gryphus* and black vultures *Coragyps atratus* expected at carcasses located in mountains (a) and plains (b). Plots are re-sampled frequency distributions obtained through randomization procedures (see text for details). Observed values of co-occurrence at carcasses are marked with a vertical arrow.



**Figure 3** Changes in male and female Andean condors *Vultur gryphus* arriving (a) and feeding (b) at carcasses located in mountains (dashed lines) and plains (solid lines) as a consequence of the increment in the number of black vultures *Coragyps atratus*. The significance of the model parameters is shown for each case.

Andean condors outnumbering black vultures in mountains, with the opposite being true in plains (species  $\times$  area:  $F_{1,3140} = 120.25$ ,  $P < 0.0001$ ; carcass as random term:  $P = 0.0015$ ).

Black vultures arrived at carcasses when female Andean condors were at low numbers ( $F_{1,416} = 21.75$ ,  $P < 0.0001$ ). Although the relationship was negative in both habitat types, this effect was exaggerated in plains compared with mountains (number of female Andean condors  $\times$  habitat:  $F_{1,416} = 3.77$ ,  $P = 0.0528$ ). No relationship was found with the number of male Andean condors ( $F_{1,413} = 0.09$ ,  $P = 0.7643$ ). However, the number of black vultures feeding was larger when both male ( $F_{1,413} = 10.68$ ,  $P = 0.0012$ ) and female ( $F_{1,416} = 6.03$ ,  $P = 0.0145$ ) Andean condors were scarce. The trends were more marked in plains than in mountains (number of male Andean condors  $\times$  habitat:  $F_{1,413} = 8.24$ ,  $P = 0.0043$ , and number of female Andean condors  $\times$  habitat:  $F_{1,416} = 9.00$ ,  $P = 0.0029$ , respectively).

The probability of male Andean condors arriving at carcasses was negatively related to the number of vultures, with differences associated with habitat type (Fig. 3a). For females, the relationship was more complex because they showed a positive association in mountains, where black vultures were scarce, and a negative association in plains, where this competitor was much more abundant (Fig. 3a).

Finally, the numbers of male and female Andean condors feeding at carcasses were negatively related to the abundance of black vultures (Fig. 3b). These effects were stronger in plains than in mountains, where black vultures were more abundant than Andean condors. Thus, even when black vultures do not completely prevent the arrival of Andean condors to carcasses, they do represent a serious obstacle to feeding when they are at high numbers.

All models of presence and abundance of Andean condors at carcasses included 'sheep carcass' as a significant random term (all  $P < 0.0244$ ). Thus, while patterns were constant across years (all  $P > 0.3592$ ), they arise even when variability among carcasses (perhaps as a consequence of their specific characteristics such as location or humanization in their surroundings) has also been recorded.

## Discussion

### Can black vultures threaten Andean condors through food competition? Inter- and intraspecific patterns

Black vultures and male Andean condors exploited carcasses with a similar temporal pattern, arriving during the

first 24 h after they were placed in the field. Conversely, female Andean condors did not show any temporal pattern of carcass use, perhaps due to their lower competitive ability, which causes them to forage with less predictability, mainly when competitors are not present in large numbers. Overall, temporal patterns in abundances of Andean condors and black vultures at carcasses underscore the ephemeral nature of scavenging opportunities (de Vault, Rhodes & Shivik, 2003) and that individuals exploiting carcasses must act quickly (Fig. 1) to avoid missing a feeding opportunity. However, the first species to arrive at carcasses was different in the two habitats considered, in agreement with their abundances. Interestingly, our models of the probability of a bird arriving at a carcass and those of the number of birds feeding showed that, although both species can exploit these resources, provided that the competitor species numbers remain low, they usually mutually avoid carcasses where the other species is feeding. Thus, the most abundant species monopolizes the resource, which is consumed mostly by one species or the other depending on the habitat considered. Like this, although a dominance hierarchy at carcasses could be related to body size (Wallace & Temple, 1987), carcass consumption seemed to be determined by species abundance, one potential mechanism precluding more damaging consequences derived from direct interspecific aggressions (Mikami & Kawata, 2004).

Although the patterns of carcass use were similar for both species, there were habitat segregations. This spatial dissociation could arise from differences in habitat preferences or tolerance for human transformations, with condors occupying mainly natural landscapes such as mountain areas, while black vultures progressively colonize human-transformed areas mainly located in plains (del Hoyo *et al.*, 1994). Moreover, Andean condors are birds at the limit of flight capacity due to high wing loading (McGahan, 1973), and individuals can have serious difficulties taking off after feeding in flat areas (Pennycuik & Scholey, 1984; Donazar *et al.*, 1999). Thus, plains could be considered as risky feeding habitats for condors because of their higher probability of being preyed by mammals or captured by humans (Pennycuik & Scholey, 1984; Donazar & Ceballos, 1988; Mundy *et al.*, 1992). On the contrary, although black vultures are currently more abundant in plains, they do not have restrictions in using mountain habitats. Indeed, they are common at high altitudes in other countries such as Peru, Bolivia or Colombia, where black vultures forage on rubbish dumps in cities that are at > 2000 m a.s.l. (Marquez *et al.*, 2005).

The evolution of some differentiation in resource use is necessary to allow for the coexistence of ecologically similar species. Among vultures of East Africa, Kruuk (1967) showed spatial and temporal segregations in their feeding behaviours, such that as the resource changed over time, species with the appropriate adaptations were able to use its various consumption stages as they occur. Moreover, he also proposed facilitatory processes among these similar species that help in the transition between these stages. Perhaps in parallel with this African guild, some studies

conducted on Cathartid vultures suggested similar patterns of food exploitation (Wallace & Temple, 1987; Lemon, 1991; Hertel, 1994). However, our results did not support the existence of resource partitioning or facilitatory processes between Andean condors and black vultures, probably because these fine-tuning mechanisms of coexistence may only be possible when ecologically similar species have a long, joint evolutionary history (Rice & Pfennig, 2008), something that appears to be lacking in this case. Certainly, the only Cathartidae present in Patagonia before European settlement were turkey vultures *Cathartes aura*, principally a solitary, less gregarious feeder (Buckley, 1997) and Andean condors (Darwin, 1839). Furthermore, the fossil record does not support a previous coexistence between Andean condors and black vultures in vast areas of their geographic ranges (Tonni & Noriega, 1988). Thus, historical factors such as the European colonization of South America may have brought about changes in the distribution of these scavengers, promoting the current coexistence of species formerly isolated in most of their geographic range (Darwin, 1839; Houston, 1985, 1988; Tonni & Noriega, 1988; del Hoyo *et al.*, 1994; Buckley, 1997; Schlee, 2000).

Both social structure and complex ecological interactions are important factors in determining the outcome of interspecific relationships. Here, we show how intraspecific aggregation through social foraging behaviour could be a potential mechanism used by black vultures to overtake interspecific competition. In our study model, the much smaller species can hoard carcasses when it is more numerous than the larger species, as currently occurs in the plains of the study area. Thus, although competition is expected to be stronger among conspecifics than heterospecifics because of their higher number of similar demands, intraspecific agonistic encounters could be less risky than face-to-face encounters with individuals of a larger species. This social facilitation of foraging among black vultures (a form of Allee effect; Reed, 1999) must be common across all of its actual distribution range, and may constitute an advantage over other, less social and/or less abundant species such as turkey vultures or, of greater concern, Andean and Californian condors (Houston, 1986; Wallace & Temple, 1987; Hiraldo, Delibes & Donazar, 1991; Lemon, 1991; Buckley, 1999; Snyder & Schmitt, 2002).

Finally, it is worth noting that sex-associated competitive asymmetries between male and female Andean condors have been described, with males dominating females and displacing them to lower quality areas (Donazar *et al.*, 1999). However, this adaptive behaviour to reduce intraspecific competition can become maladaptive under current situations. Indeed, female Andean condors suffered both intraspecific competition by dominant males, which segregate them to low-quality areas (plains, Donazar *et al.*, 1999), and interspecific competition by black vultures, which are much more numerous in human-transformed habitats (plains), reducing their probabilities of arriving and feeding at carcasses. Higher mortality risks associated with the use of more human impacted areas and lower feeding efficiency linked to the presence of a superior competitor might result

in a sex-biased population imbalance for Andean condors that may pose difficulties in mating and reproduction (Reed, 1999). Data from Southern Chile (Sarno, Franklin & Prexl, 2000) and Argentina (authors unpubl. data) show that the sex ratio of juvenile Andean condors was unbiased or at most significantly skewed in favour of females ( $\text{♂}:\text{♀}$ , Argentina: 1:1.37; Chile: 1:2.21), while that of adults was significantly skewed in favour of males (Argentina: 1:0.55; Chile: 1:0.71). Although not conclusive, these results suggest potential sexual biases in mortality rates (Sarno *et al.*, 2000), lending support to our results.

### Conservation implications

Potential threats to the long-term conservation of Andean condors can arise when considering the expansion of black vultures, a strong competitor that can hamper carcass exploitation when it is in larger numbers than condors. This scenario of interspecific competition can be of greater concern when it is transferred to other regions of the northern range of the Andean condor's distribution, such as Ecuador (*c.* 65 birds in five disjunct populations; BirdLife International, 2008*b*), Venezuela (<30 individuals; Cuesta & Sulbaran, 2000) or Colombia (180 individuals), where this species is becoming more rare compared with black vultures, which are increasingly more common at high altitudes following human populations (del Hoyo *et al.*, 1994; BirdLife International, 2008*a*). Thus, competition for food with black vultures can pose serious problems to the success of many management actions and reintroduction programmes of condors which involve considerable effort by the private and governmental sectors (Díaz *et al.*, 2000; BirdLife International, 2008*b*). The management of black vultures, perhaps through the management of human-provided feeding sources, should be considered as a complementary action within the Andean condor conservation programme. Broadly, similar situations should be envisaged when considering the more endangered Californian condor, which was nearly extinct (Cohn, 1999) and now is at very low numbers in the wild. Although Californian condors are currently only in natural areas of the US where black vultures are rare or accidental, care must be taken with the creation of feeding points for this endangered species or with human establishments in this zone because these activities can facilitate the expansion of the black vulture.

In a scenario of global change and biotic homogenization in which human disturbance plays a major role (Vitousek *et al.*, 1997; Olden *et al.*, 2004; Ricciardi, 2007), many winning species can be favoured to establish and spread through new anthropogenic habitats, representing an important threat to other, more human-sensitive species that could be superior competitors in more natural areas but not always in the transformed areas (Didham *et al.*, 2007). Mooney & Cleland (2001) pointed out that extinction by competition is a slow process not likely to be observed on the time scale of most scientific studies. However, changes in the relative abundance of biomasses among species (*i.e.* evenness) can occur rapidly, and can have important con-

sequences for ecosystems long before a species is threatened by extinction (Chapin *et al.*, 2000). Although our findings do not allow us to establish a causal relationship between the expansion of black vultures and the reduction, and potentially long-term extinction through competition, of Andean condors, they suggest that the expansion of this winning species is triggering interspecific competition with a species with negative response towards human activities (del Hoyo *et al.*, 1994; Speziale *et al.*, 2008). Moreover, we cannot discard the fact that the decline of Andean condors can also in some way favour the expansion of black vultures. Thus, both processes, invasion through range expansion and extinction, could be occurring and can result in the reduction of the diversity, the  $\beta$  diversity, of the scavenger guilds in the New World. Currently, there is at least a change in the relative abundances of both species following human activities, and further research is needed to establish whether interactions within the scavenger guild have been altered or ecosystem processes have been modified through fluxes of energy and materials (Chapin *et al.*, 2000).

Our study suggests that potential negative responses of some scavenger species such as Andean condors resulting from an increase in the number and range distribution of black vultures represent ecologically plausible scenarios. Of course, the validity of this proposed model of competitive exclusion to other species necessitates further research. For the time being, we simply advocate that managers and conservationists take this possibility into account when developing management schemes for the long-term conservation of these emblematic vertebrates.

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