Trophic niche overlap among scavengers in Patagonia supports the condor-vulture competition hypothesis

FERNANDO BALLEJO, SERGIO A. LAMBERTUCCI, ANA TREJO and
LUCIANO J. M. DE SANTIS

Summary

Animals that share resources tend to use different foraging strategies in order to decrease potential competition. Scavenging birds using the same nutritional resources can segregate into different space and time scales. However, it has been suggested that when the species do not co-evolve to achieve such segregation competition may result. Our aim was to study the trophic niche overlap between three species of obligate scavengers, the Andean Condor *Vultur gryphus*, Turkey Vulture *Cathartes aura* and American Black Vulture *Coragyps atratus*, which are the main avian consumers of carcasses in north-western Patagonia. Black Vultures arrived in the area relatively recently, have expanded their distribution following human activities, and have been suggested to compete with the threatened condor. We collected pellets in communal roosts of the three species to determine their diet, and to estimate the diversity (Shannon Index) and diet similarity (Pianka overlap index). We found that the Turkey Vulture has greater niche breadth and, apart from domestic livestock, it incorporates smaller items such as fish, reptiles and a great number of birds, carnivores and mice. Although the Black Vulture diet includes arthropods, they feed primarily on introduced ungulates, overlapping more with condor diet when roosting far from urban centres. As these latter two species share the same food resource, human activities that positively affect the abundance of the Black Vulture could increase competition among them, with possible implications for the conservation of the Andean Condor.

Introduction

One of the most important daily challenges that birds must face is the discovery, consumption and use of energy sources. To do so, they must keep a balance between the costs generated to obtain energy and the energy gain (Pianka 1985, Gutiérrez 1998). One of the strategies used by animals to reduce the costs of competition is to occupy different ecological niches. In this respect, using different strategies to avoid competition, they differ in what to eat, where to get food and when to seek food. If these strategies overlap, resource competition may occur; this is detrimental for both parties and can eventually trigger the extinction of one of them (Pianka 1985).

Traditionally, food web studies have not considered scavengers (Wilson and Wolkovich 2011). Carrion is available episodically, as a pulsating resource that can vary seasonally and spatially, playing a dynamic role in the stability of food webs, and the movements and distribution of species that feed on it (Wilson and Wolkovich 2011, Barton *et al.* 2013). The stable coexistence of different scavengers on the same carcass is only possible if there is a partition of the resource, allowing the different species to be segregated in space and time when they feed from the same source. To maintain coexistence in equilibrium the intervening species may need to adapt

anatomically and behaviourally to reduce food-niche overlap (Houston 1988, Arjo and Pletscher 1999, Prior and Weatherhead 2004, Blázquez *et al.* 2009, Moreno-Opo *et al.* 2016). Even so, if the resource is scarce, competition can allow more aggressive species to monopolise food and possibly to increase, displacing the other species (Hiraldo *et al.* 1991a, Stolen 1996).

In north-western Patagonia, carrion is used by several avian scavengers of different sizes (Del Hoyo *et al.* 1994). The three most important scavengers in the area are representatives of the Cathartidae family (Order Cathartiformes): the Andean Condor *Vultur gryphus*, Turkey Vulture *Cathartes aura* and American Black Vulture *Coragyps atratus*. Other birds which also use this type of food belong to the family Falconidae (Order Falconiformes, e.g. *Milvago chimango* and *Caracara plancus*), but the latter only do so facultatively (Del Hoyo *et al.* 1994). Therefore, at least among obligate scavengers, there could be competition for such a fleeting and random resource as carrion, especially if an imbalance in abundance occurs which favours one species over others (Cortés-Avizanda 2010, Cortés-Avizanda *et al.* 2012). The variables that could have an impact on this balance are: the location of the roosts (Hiraldo *et al.* 1991a, Ballejo and De Santis 2013, Novaes and Cintra 2013), topography (Carrete *et al.* 2010), proximity to human structures (Lambertucci *et al.* 2009a, Novaes and Cintra 2013), weather conditions that facilitate access to carrion (Shepard and Lambertucci 2013) and hierarchy (Houston 1988). As there is a hierarchy in access to the carrion by size, the largest avian scavenger Andean Condor (c.12 kg) displaces smaller scavenging birds (Wallace and Temple 1987). However, it has been documented that the number of condors feeding on a carcass decreases relative to the abundance of Black Vultures (Carrete *et al.* 2010).

Food availability resulting from human activities such as garbage dumps, slaughterhouses and fishing discards are a source of predictable resources in space and time that Black Vultures take advantage of, leading to increases in population size (Houston 1988, Campbell 2014, Barbar *et al.* 2015). Previous work with Old World vultures has shown that, in areas where human activities generate a temporal and spatial predictability of carcass disposal, there is a decrease in the diversity of scavengers, as opposed to areas where carrion remains unpredictable. In these scenarios species richness remains constant, but not taxonomic diversity, so individuals of dominant species are present in greater numbers. (Wilmers *et al.* 2003, Cortés-Avizanda *et al.* 2012, Oro *et al.* 2013).

The Black Vulture and the Andean Condor feed mainly on domestic livestock (Lambertucci *et al.* 2009b, Ballejo and De Santis, 2013), whereas the Turkey Vulture has a wider diet (Hiraldo *et al.* 1991b). However, there have been no comparative studies on their diet overlap in the same area. Therefore, our aim is to analyse and compare the diet of three obligate scavenger species from north-western Patagonia, by analysing the overlap of trophic niche from their pellets. We expect a greater degree of trophic niche overlap between Black Vulture and Andean Condor, compared with the Turkey Vulture, mainly in places far from the urban development, which will be further support for the scenario of competition between those species.

Materials and methods

Study area

The study area lies in north-western Argentine Patagonia, southern tip of South America (36°–41°S and 71°–68°W) (Figure 1). The climate is cold-temperate, with frequent snowfall in winter and with summer being the driest season (Paruelo *et al.* 1998). The study area encompasses almost 100,000 km² and includes a mosaic of woodlands and steppes that forms a heterogeneous landscape. The geological and climatic history, along with more recent erosive processes, have created a large number of cliffs that are used as communal roosts by condors. Cliffs and forests are used by vultures as communal roosts (Del Hoyo *et al.* 1994). The area has been used for extensive livestock ranching since the last century, and is also one of the regions in Argentina that received the greatest amount of exotic mammal introductions, including Red Deer *Cervus elaphus*, Wild Boar *Sus scrofa*,
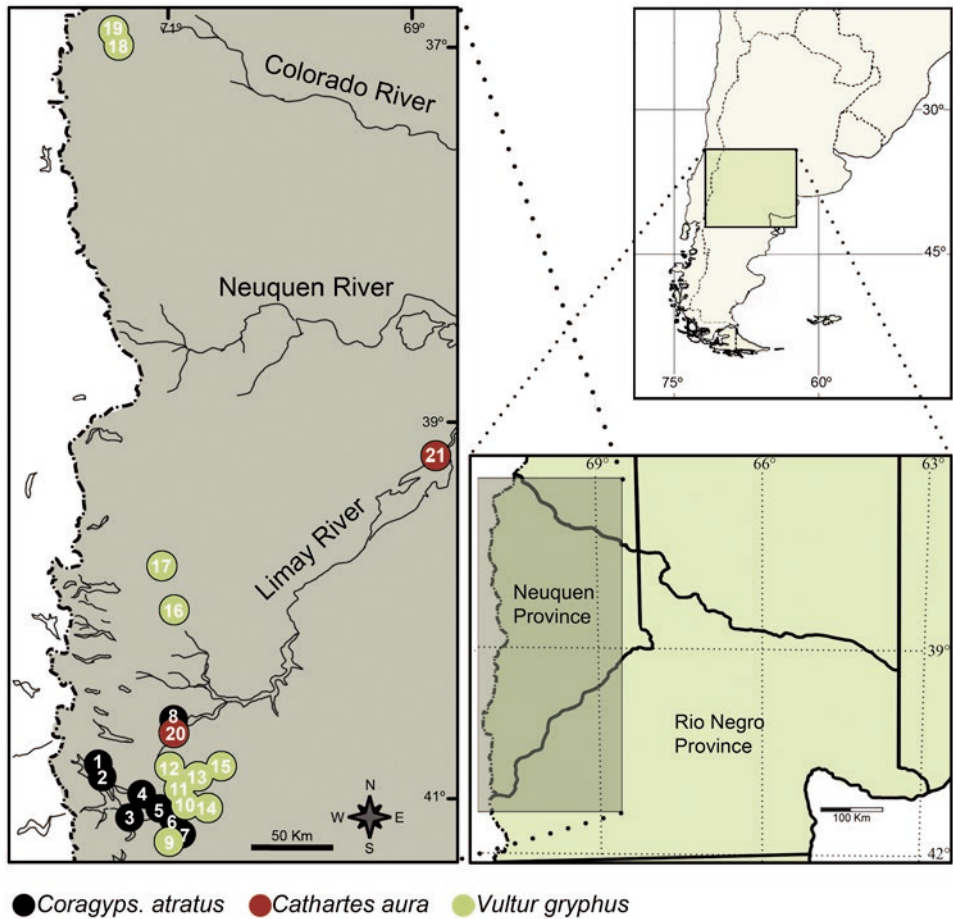
Figure 1. Diagram of the study area and location of each species roost found. 1. Estacas, 2. Victoria, 3. Coihues, 4. Jones, 5. Dina Huapi, 6. Cóndor II, 7. Cóndor I, 8. Chacabuco I, 9. Buitrera, 10. Fg. Chica, 11. Fg. Grande, 12. Condorerita, 13. Pipilcurá, 14. Pichileufú, 15. Chaqueñita, 16. Huechaue, 17. Remolinos, 18. Guanaco, 19. Covunco, 20 Chacabuco II, 21. Chocón.

European Hare *Lepus europaeus*, and Rabbit *Oryctolagus cuniculus* (Novillo and Ojeda 2008, Speziale *et al.* 2012). Those species have been reported as part of the scavengers' diet (Lambertucci *et al.* 2009b, Ballejo and De Santis 2013).

Study species

We studied three species of obligate scavengers. The Andean Condor (female: 8–11 kg; male: 11–15 kg) feeds in Patagonia, southern South America, mainly on domestic ungulates (Lambertucci *et al.* 2009b) Roosting and nesting occur in mountains (on cliffs, and rock shelters) and foraging occurs in open areas - steppes, grasslands, and beaches along the coast (Del Hoyo *et al.* 1994, Lambertucci *et al.* 2014). It is a species of large dimensions, which displaces smaller species from access to carrion. Due to its large and efficient bill it can open the abdominal cavity of large ungulates, providing access to the viscera for other birds of lower rank (Wallace and Temple 1987, Del Hoyo *et al.* 1994). The study area has one of the best condor populations known (more than 250 individuals;

Lambertucci 2010). The Turkey Vulture (0.85–2.0 kg) roosts socially on cliffs, rock shelters, and trees. They feed on carcasses of different sizes, soaring at low altitudes in small groups and mainly using their sense of smell, allowing them to locate small carcasses, which are consumed quickly, before other members of the guild arrive (Houston 1988, Thomaides *et al.* 1989, Hiraldo *et al.* 1991b, Buckley 1997). There are no current estimations of the population size or trends of this species in the area. The Black Vulture (1.1–1.9 kg) inhabits open areas and roosts on cliffs, rock shelters, or trees. It forages and feeds socially in large groups, and searches for food using the sense of sight (Houston 1988, Stolen 1996). It feeds on carcasses of different sizes (Coleman and Fraser 1989) and is favoured by human activities that gather organic matter in places like garbage dumps and slaughterhouses (Iñigo Elías 1987, Ballejo and De Santis 2013). Black Vulture arrived in the area relatively recently and has expanded its distribution following human activities. Houston (1985, 1988) notes that Black Vulture is more abundant in open habitats near human settlements of at least 3,000 people. He also suggests that before the human settlement of South America, Black Vultures were probably restricted to open savannas, swamplands and large river banks, feeding on large mammals, stranded fish, and smaller food items. This range expansion is evidenced in the literature (Darwin 1839, Houston 1985, 1988, Tonni and Noriega 1988, Buckley 1997). Current studies show the greatest abundance of Black Vultures in urban and semi-urban areas (Bellati 2000, Campbell 2014, Barbar *et al.* 2015). There is no study analysing the expansion of the population in the study area, however, these populations have probably increased in parallel with urbanisation processes as in other regions (Del Hoyo *et al.* 1994, Campbell 2014).

Diet survey

During the summer of 2012, we collected vulture pellets from communal roosts to analyse the composition of the diet. The analysis of pellets is one of the most used methods to study bird of prey diet; however, this method overestimates the bone remains of smaller prey. In contrast, skeletal remains found in the nest overestimate the larger prey. Vulture pellets mainly have hair. Therefore this method is reliable with an adequate knowledge of the fauna in the area, good comparison collections, and the application of microscopy techniques (Real 1996).

Pellets were collected from: a) Eight Black Vulture roosts; four of them characterised by being on trees in Patagonian steppe, near livestock farms in an area that has been used for extensive livestock of sheep, and away from urban centres (Chacabuco I, Condor I, Condor II and Jones); and the last four characterised by being near or within urban areas: the Estacas roost is less than 2 km from a garbage dump; the Victoria roost is on abandoned buildings; and the Coihues and Dina Huapi roosts are on trees within villages with these names; b) two Turkey Vulture roosts, one of them is on trees in rural context near a trout farm (Chacabuco II), and the other is on trees inside a town (Chocón); and c) 11 Andean Condor roosts; which are on cliffs in a natural environment in the Patagonian steppe. Location of roosts is shown in Figure 1. Roosts were classified as rural context (rural and natural environments located more than 15 km from an urban area) and urban context (located within or less than 2 km from an urban area).

Bone and teeth were separated and studied under a stereoscopic microscope (10–40 x). Bone remains were identified using reference materials from the collection at the Museum of Natural Science of La Plata (Buenos Aires Province). Moreover, hair remains were identified using cuticular and medullary patterns with optical microscopy, and using reference materials from the collection at the Museum of La Plata, and the collection of "Patagonia Vertebrate inventory" from the National Parks Administration (Administración de Parques Nacionales, Argentina), as well as with bibliographic sources (Chehébar and Martín 1989, De Marinis and Asprea 2006). Feathers and arthropod heads were identified by comparison with a reference collection from the Museum of La Plata, Buenos Aires (Argentina).

In the case of the Andean Condor roosts, samples collected in 2007 and in this study in 2009 were pooled. The 2007 data was published in a previous work, corresponding to the same study area (Lambertucci *et al.* 2009b). To confirm that there has been no change in diet over the years regarding the pellets collected for this work, we applied the Pianka index of trophic niche overlap

(O $_{j, k}$ = Σp$_{ij}$ applied. P$_{ik}$ / √ (Σp$_{ij}$2. Σp$_{ik}$2) (Pianka 1973), where p$_{ij}$ and p$_{ik}$ are the proportion of the prey type "i" in the diet of the "j" and "k" species respectively. This index yields values from 0 (no overlap) to 1 (complete overlap) and we did not find any differences (O $_{j, k}$ = 0.985).

We used the minimum number of individuals (MNI) based on the bone elements found in pellets (Grayson 1978). In the cases in which they were not found, hair, feathers and / or scales were counted, considering one individual per pellet; arthropods were quantified based on their heads. In all cases species found were identified at the lowest possible taxonomic level.

Data analysis

We expressed our results on diet composition as a percentage of the total prey (representing the number of times each item was encountered in relation to the overall number of items in all pellets), and percentage occurrence of each item in relation to the overall number of pellets. Diet diversity was calculated using the Shannon index, H '= -Σp$_i$log2p$_i$, and we used Pianka's index (Pianka 1973) to compare dietary overlap. From the results of this last index, we created a dendrogram using the statistical software PAST (Paleontological Statistics) version 3.02. The graphic display of this analysis shows clusters in relation to the similarities in the taxa ingested by individuals of each roost. Finally, we carried out a correspondence analysis to examine the relationship between the environment where the roosts were located and the taxa consumed. This type of analysis aims to represent each of the possible values for each variable, where the relative position of the points reflects the degree of association between each of the concepts represented. To perform this analysis a contingency table was drawn up where taxa ingested were placed in rows, and scavenger species in columns, and separated in relation to the environment where their roosts are located (rural or urban context). We used RStudio program (pgirmess package) for this statistical analysis (Giraudoux and Giraudoux 2015).

Results

The three species studied consume carrion of large ungulates (mainly sheep) and hares. In turn, vultures also eat other mammals such as canines, where the genus *Lycalopex* was the most represented in the pellets in addition to weasels (Mustelidae), felines and cricetid rodents (Table 1). However, vultures also prey on arthropods. The most representative arthropods in the samples were Coleoptera (Tenebrionidae), Hymenoptera and the Orthoptera (Formicidae). But among Coleoptera, the fmailies Scarabaeidae, Carabidae, Elateridae and Curculionidae were also found, in addition to representatives of the order Blattodea and the Chelicerata (family Bothriuridae). In turn, synthetic materials such as polyethylene bags, rubber bands and rubber were also found in vulture pellets. Turkey Vulture has the highest diet diversity, as their sample includes both large ungulates and reptiles as well as teleost fishes and a large number of birds and carnivores. The lowest diversity value is found in the samples of Andean condor, which feeds mainly on domestic ungulates and hares (Table 2).

The dendrogram shows the similarity between prey type consumed among each roost (Figure 2). Three main groups were found, one of which contains only the Andean Condor roosts; the second contains Black Vulture roosts, characterised by being located away from urban centres and near livestock farms; the last group contains the remaining roosts belonging to both species of vultures, most of which are near or within urban centres. However, in this last group there is a clear segregation between both species of vultures. Moreover, the first two groups share a higher degree of similarity to each other (0.4–0.5) than with the third (0.2–0.3).

Associations between variables considering the closeness that each of the points in the correspondence analysis (Figure 3) were in agreement with the dendrogram (Figure 2). Black Vultures in a rural context have a similar diet to the Andean Condor, with *Lepus europaeus, Ovis aries* and *Cervus elaphus* the taxa with the highest incidences. Black Vultures in urban areas differ from the previous group, with *Bos taurus* and *Sus scrofa* being the most frequent prey items. On the other

Table 1. Diet composition of three scavenger species in northwestern Patagonian. We present the number of prey items (n) Frequency percentage (F%) corresponds to the percentage of the total number of taxa. Percentage of occurrence (O%) is the percentage of the total number of pellets.

TAXA	*Cathartes*			*Coragyps*			*Vultur*		
	n	%F	%O	n	%F	%O	n	%F	%O
Teleostei	4	2,21	4,17	0	0	0	0	0	0
Reptilia	13	7,18	13,5	0	0	0	0	0	0
Bird (indet.)	35	19,3	36,5	46	5,95	13,4	10	1,34	1,85
Galliforme	9	4,97	9,38	3	0,39	0,87	0	0	0
Passeriforme (indet.)	4	2,21	4,17	0	0	0	0	0	0
Carduelis sp.	0	0	0	1	0,13	0,29	0	0	0
Mammalia (indet.)	11	6,08	11,5	54	6,99	15,7	7	0,94	1,29
Ungulata (indet.)	3	1,66	3,13	8	1,03	2,33	0	0	0
Bos taurus	15	8,29	15,6	92	11,9	26,7	59	7,91	10,9
Ovis aries	4	2,21	4,17	89	11,5	25,9	395	52,9	72,9
Cervus elaphus	7	3,87	7,29	45	5,82	13,1	102	13,7	18,8
Sus scrofa	1	0,55	1,04	5	0,65	1,45	2	0,27	0,37
Lama guanicoe	1	0,55	1,04	0	0	0	3	0,4	0,55
Felidae	2	1,1	2,08	0	0	0	0	0	0
Canis familiaris	1	0,55	1,04	9	1,16	2,62	0	0	0
Lycalopex sp.	17	9,39	17,7	0	0	0	0	0	0
Conepatus sp.	3	1,66	3,13	0	0	0	0	0	0
Lepus europaeus	11	6,08	11,5	83	10,7	24,1	168	22,5	31
Cricetidae	6	3,31	6,25	3	0,39	0,87	0	0	0
Reithrodon auritus	0	0	0	1	0,13	0,29	0	0	0
Artrophoda	12	6,63	8,33	292	37,8	28,8	0	0	0
Sintetic	22	12,2	22,9	42	5,43	12,2	0	0	0
Total prey		181			773			746	
Number of pellets		96			344			542	

hand, Turkey Vulture roosts are found in both kinds of habitat (rural and urban) and they showed the highest diversity. This is mainly because they are the only species in which reptiles and fish occur in their pellets, and they feed on a higher proportion of felines, canines and cricetid rodents than the other two species (see Table 1).

Discussion

To maintain a demographic balance between populations in a community, species occupy certain trophic niches and have specific foraging strategies. When they move away from this balance, an increase in the trophic niche overlap might take place, increasing competition for resources (Pianka 1985). Our results indicate that such overlaps exists to a significant degree between the Black Vulture and the Andean Condor in rural areas, but not with the Turkey Vulture. The Andean Condor and the Black Vulture feed primarily on domestic livestock carrion (Lambertucci *et al.* 2009b, Ballejo and De Santis 2013, this study). Moreover, they showed higher trophic niche overlap when roosting in a similar context (i.e. they feed on similar food sources when they are far from cities, in a rural context). The Turkey Vulture feeds on the widest range of carrion, regardless of where the roosts are sited, incorporating fish, reptiles and a larger number of birds, carnivores and mice in their diet. As a result, the trophic niche overlap with the other two species is reduced. The difference in selection of carrion might be due to the developed sense of smell which is characteristic of this bird, and which allows them to find carcases of a size that would go unnoticed by the other two species, that mainly use the sense of sight for this purpose (Houston 1988). Moreover, their ability to fly at low altitudes allows them to seek alternative sources of food (Coleman and Fraser 1989, Stolen 2000).

Table 2. Shannon diversity index calculated on the basis of the diet in different communal roosts for three species of scavengers (Cathartidae family)

Species	Roost	Shannon index
Cathartes aura	Chacabuco II	2,613
	Chocón	2,396
Coragyps atratus	Estacas	2,135
	Cóndor II	2,087
	Jones	2,072
	Cóndor I	2,004
	Chacabuco I	2,003
	Coihues	1,97
	Victoria	1,96
	Dina Huapi	1,547
Vultur gryphus	Condorerita	1,348
	Buitrera	1,24
	Pichileufu	1,021
	Huechahue	1,013
	Fg. Chica	0,9844
	Fg. Grande	0,9539
	Pipilcurá	0,8442
	Chaqueñita	0,8131
	Guanaco	0,4101
	Covunco	0,3708
	Remolinos	0,1217

Black Vulture roosts located in rural areas showed a greater diversity than those in urban areas. An exception is the Estacas roost, which is located near a rubbish dump. The use of garbage as food is well documented in scavengers (Plaza and Lambertucci 2017). In those places the diversity of food sources and its availability have a positive effect on the development of their populations (Plaza and Lambertucci 2017, Steigerwald *et al.* 2015). Differences in diversity of taxa consumed in rural and urban roosts of Black Vulture have been previously documented, with cows and sheep as the main prey consumed, whereas in rural roosts, hares and a large number of arthropods replace that domestic food source (Ballejo and De Santis, 2013). Furthermore, we can assert that the Turkey Vulture has a higher prey diversity in both roosts studied, as found by other authors (Hiraldo *et al.* 1991b). The Andean Condor tends to occur far from human-occupied areas (Speziale *et al.* 2008). It has the lowest value in food diversity since they feed almost exclusively on domestic and wild exotic species in rural environments (Lambertucci *et al.* 2009b).

The Old World scavengers are temporally and spatially segregated in the use of carrion (Kruuk 1967, Blázquez *et al.* 2009, Cortés-Avizanda 2010, Kendall *et al.* 2012, Moreno-Opo *et al.* 2016). Once they find a carcase, they can dominate birds of lower rank. However, smaller birds can sometimes benefit from their presence as they dismember large corpses (Kruuk 1967, Moreno-Opo *et al.* 2015). The random distribution of carcases plays a key role, because where carcases are concentrated in small areas, the diversity of scavengers is affected, leaving the resource to be monopolised by the largest and most abundant species (Cortés-Avizanda *et al.* 2012). On the other hand, they show differences in bill morphology and pecking activity (number of pecks through time), allowing them to specialise in the exploitation of different body parts (Kruuk 1967, Moreno-Opo *et al.* 2016). This facilitates coexistence between species. Similarly, New World vultures (Cathartidae) have a clear size hierarchy, in which the larger birds typically displace the smaller (Wallace and Temple 1987, Houston 1988, Hertel 1994). However, when the number of individuals is unbalanced, these hierarchies can be lost (Buckley 1996, Carrete *et al.* 2010). In this sense, Turkey Vultures and Andean Condors could be displaced from carcases when Black Vultures appear in large numbers. Despite this, Turkey Vultures can diversify their diet to
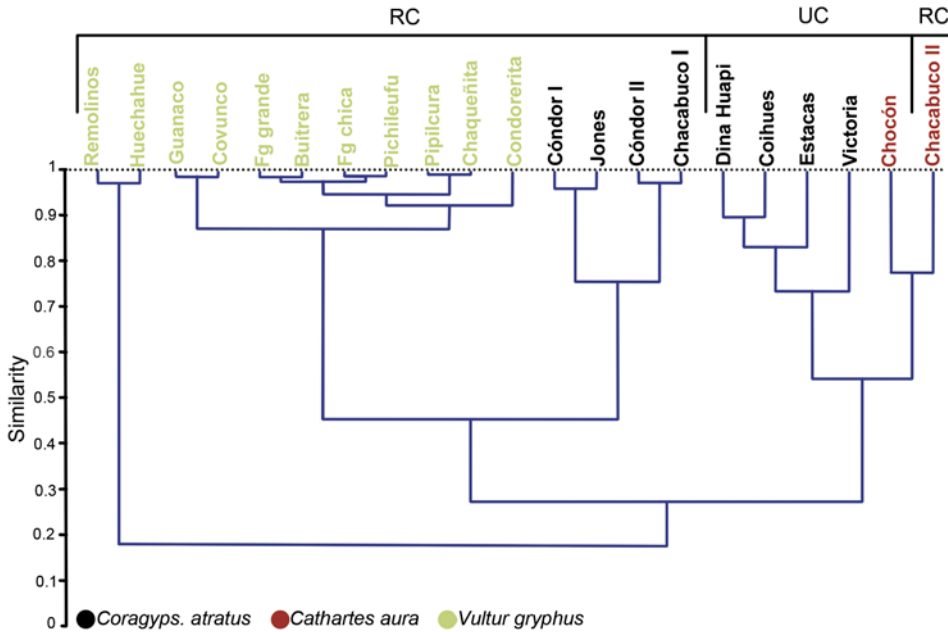
Figure 2. Dendrogram based on the Pianka index of trophic niche overlap of the diet of three species of scavengers surveyed in their communal roosts. Roosts were located in Rural context (RC) or Urban context (UC).

incorporate bodies of smaller animals (Hiraldo *et al.* 1991c). This does not happen with the Andean Condor, probably because small animals hardly cover their nutritional needs (Donázar *et al.* 2010). This would be less likely to affect Andean Condor populations if both species consumed different taxa or had extensive dietary diversity. However, our results indicate that both species consume similar taxa in areas of sympatry, which supports the idea that Andean Condor populations could be adversely affected if the number of Black Vultures increased (Carrete *et al.* 2010).

The ability to feed on anthropogenic waste is evidenced by the presence of synthetic materials found in the pellets of Black Vultures in this study, as well as in previous works (Iñigo Elías 1987, Sazima 2007, Ballejo and De Santis 2013). Therefore, a scenario of asymmetric competition may arise, with Black Vultures benefiting from the presence of alternative and predictable food resources generated by human activities (Novaes and Cintra 2013). This could be the reason why this species has become increasingly common in urban environments (Novaes and Cintra 2013, Campbell 2014), extending its distribution and abundance to areas occupied by the Andean Condor (Bellati 2000, Barbar *et al.* 2015). This type of anthropogenic resource is not used by the Andean Condor in the area, as it is very sensitive to urbanisation (Speziale *et al.* 2008, Lambertucci *et al.* 2009a), nor in most of its distribution range (except in one place in Central Chile). Condor populations have been affected to a different extent in different countries, becoming in danger of extinction in Colombia, Ecuador and Venezuela (Lambertucci 2007). In Argentina their populations are more numerous (Lambertucci 2010), but face a series of threats, including persecution, ingestion of toxic baits and pesticides, poisoning by ingestion of lead ammunition, and collision with power lines (Lambertucci 2007, Lambertucci *et al.* 2011). This situation places the Andean Condor in a vulnerable position which could worsen in the presence of numerous populations of Black Vultures (Carrete *et al.* 2010).
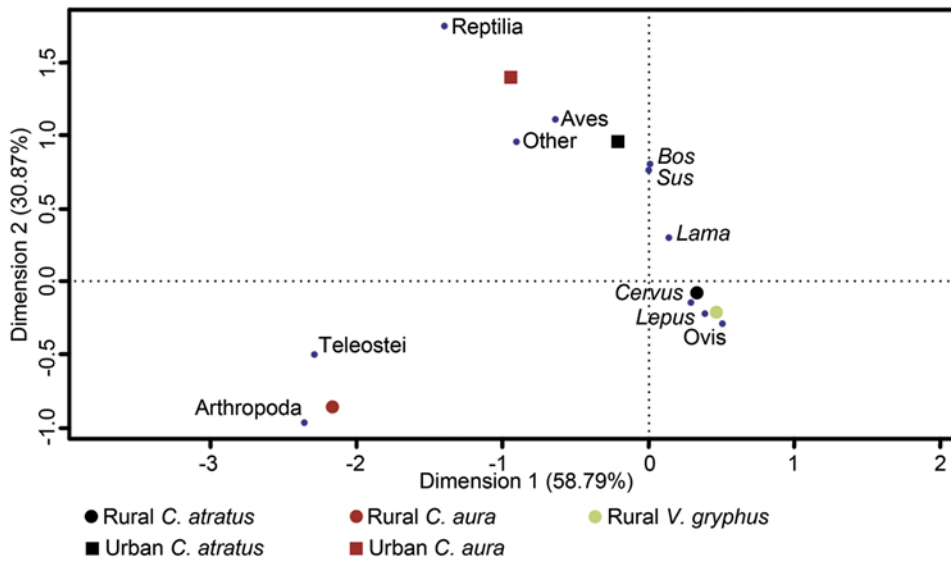
Figure 3. Correspondence analysis showing the ingested taxa (points) and scavenger species (geometric figures) separated by the environment where their roosts are located. The "other" category includes felids, canids and cricetid rodents.

The presence of resources resulting from human activities, which are predictable in space and time (e.g. landfill), has direct effects on individuals, but also generates cascade effects on populations and communities worldwide (Oro *et al.* 2013, Plaza and Lambertucci 2017). The effects on birds are diverse, for example by generating changes in their home-ranges, since they are limited to areas where food is located (Monsarrat *et al.* 2013); and altering nesting and roosting areas, since these are selected for proximity to sources of food (Kristan and Boarman 2007, Selva and Fortuna 2007). They can generate a dependency on the resource, so a lack of can trigger sharp declines in the populations that profit from it (Oro *et al.* 2008) and they can diminish the diversity of communities, since the resource can be monopolised by more aggressive species (Cortés-Avizanda *et al.* 2012, Plaza and Lambertucci 2017). But one of the main consequences is that these resources can facilitate the emergence of native invader species, since the availability of readily available food can increase the population of species that can best take advantage of this resource in comparison to others (Carey *et al.* 2012; Oro *et al.* 2013, Plaza and Lambertucci 2017). These species might have a similar impact to that caused by alien invader species, which through various mechanisms such as competition, can alter the structure of a community and in severe cases reduce or eliminate populations of native species (Carey *et al.* 2012). Black Vultures show the typical characteristics of a native invader species, with environmental changes generated by human activities facilitating population growth, increasing their survival and reproduction. Therefore, they can take advantage of the vacancies left by other native species that suffer a loss or decline of their populations because of these activities (Carey *et al.* 2012). This kind of competition favoured by human activities should to be incorporated in conservation strategies, particularly those aiming to conserve the most vulnerable and less flexible species to anthropogenic advance.

Acknowledgements

References

Arjo, W. M. and Pletscher, D. H. (1999) Behavioral responses of coyotes to wolf recolonization in northwestern Montana. *Can. J. Zool.* 1927: 1919–1927.

Ballejo, F. and De Santis, L. J. M. (2013) Dieta estacional del jote cabeza negra (*Coragyps atratus*) en un área rural y una urbana. *Hornero* 28: 7–14.

Barbar, F., Werenkraut, V., Morales, J. M. and Lambertucci, S. A. (2015) Emerging ecosystems change the spatial distribution of top carnivores even in poorly populated areas. *PLoS One* 10: 1–12.

Barton, P. S., Cunningham, S. A, Lindenmayer, D. B. and Manning, A. D. (2013) The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia* 171: 761–72.

Bellati, J. (2000) Comportamiento y abundancia relativa de rapaces de la Patagonia Extrandina Argentina. *Ornitol. Neotrop.* 11: 207–222.

Blázquez, M., Sánchez-Zapata, J. A., Botella, F., Carrete, M. and Eguía, S. (2009) Spatio-temporal segregation of facultative avian scavengers at ungulate carcasses. *Acta Oecologica* 35: 645–650.

Buckley, N. J. (1996) Food finding and the influence of information, local enhancement, and communal roosting on foraging success of North American vultures. *Auk* 113: 473–488.

Buckley, N. J. (1997) Experimental tests of the information-center hypothesis with black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*). *Behav. Ecol. Sociobiol.* 41: 267–279.

Campbell, M. O. N. (2014) The impact of urbanization and agricultural development on vultures in El Salvador. *Vulture News* 66: 16–28.

Carey, M. P., Sanderson, B. L., Barnas, K. A and Olden, J. D. (2012) Native invaders – challenges for science, management, policy, and society. *Front. Ecol. Environ.* 10: 373–381.

Carrete, M., Lambertucci, S. A., Speziale, K., Ceballos, O., Travaini, A., Delibes, M., Hiraldo, F. and Donázar, J. A. (2010) Winners and losers in human-made habitats: interspecific competition outcomes in two Neotropical vultures. *Anim. Conserv.* 13: 390–398.

Chehébar, C. and Martín, S. (1989) Guía para el reconocimiento microscópico de los pelos de los mamíferos de la Patagonia. *Acta Vertebr.* 16: 247–291.

Coleman, J. S. and Fraser, J. D. (1989) Habitat use and home ranges of black and turkey vultures. *J. Wildl. Manage.* 53: 782–792.

Cortés-Avizanda, A. (2010) *Efectos ecológicos de la heterogeneidad espacial y predecibilidad en la distribución de los recursos: carroñas y gremios de carroñeros*. Madrid, Spain: Universidad Autónoma de Madrid.

Cortés-Avizanda, A., Jovani, R., Carrete, M. and Donázar, J. A. (2012) Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: A field experiment. *Ecology* 93: 2570–2579.

Darwin, C. (1839) *Narrative of the surveying voyages of His Majesty's ships Adventurer and Beagle, between the years 1826 and 1836*. London, UK: Coribun.

De Marinis, A. M. and Asprea, A. (2006) Hair identification key of wild and domestic ungulates from southern Europe. *Wildlife Biol.* 12: 305–320.

Del Hoyo, J., Elliott, A. and Sargatal, J. (1994) *Handbook of the birds of the world. New World Vultures to Guineafowl,* Lymx Editions, Barcelona.

Donázar, J. A., Cortés-Avizanda, A. and Carrete, M. (2010) Dietary shifts in two vultures after the demise of supplementary feeding stations: consequences of the EU sanitary legislation. *Eur. J. Wildl. Res.* 56: 613–621.

Giraudoux, P. and Giraudoux, M. P. (2015) Package 'pgirmess'. See https://cran.r-project.org/web/packages/pgirmess/.

Grayson, D. K. (1978) Minimum numbers and sample size in vertebrate faunal analysis. *Am. Antiq.* 43: 53–65.

Gutiérrez, G. (1998) Estrategias de forrajeo. Pp. 359–381 in R. Ardila, W. López, A. M. Pérez, R. Quiñones and F Reyes, eds. *Manual de análisis experimental del comportamiento*. Madrid, Spain: Librería Nueva.

Hertel, F. (1994) Diversity in body size and feeding morphology within past and present vulture assemblages. *Ecology* 75: 1074–1084.

Hiraldo, F., Blanco, J. C. and Bustamante, J. (1991a) Unspecialized exploitation of small carcasses by birds. *Bird Study.* 38: 200–207.

Hiraldo, F., Delibes, M., Bustamante, J. and Estrella, R. R. (1991b) Overlap in the diets of diurnal raptors breeding at the Michilia Biosphere Reserve, Durango, Mexico. *J. Raptor Res.* 25: 25–29.

Hiraldo, F., Delibes, M. and Donazar, J. A. (1991c) Comparison of diets of Turkey Vultures in three regions of Northern Mexico. *J. Field Ornithol.* 62: 319–324.

Houston, D. C. (1985) Evolutionary ecology of Afrotropical and neotropical vultures in forests. In P. Buckley, M. Foster, E. Morton, R. Ridgley and F. Buckley, eds. *Neotropical ornithology*, American Ornithologists Union. Washington D.C. pp. 6–864.

Houston, D. C. (1988) Competition for food between Neotropical vultures in forest. *Ibis* 130: 402–417.

Iñigo Elías, E. E. (1987) Feeding habits and ingestion of synthetic products in a black vulture population from Chiapas, Mexico. *Acta Zool. Mex.* 22: 1–15.

Kendall, C. O. K., Virani, M. Z., Kirui, P., Thomsett, S. and Githiru, M. (2012) Mechanisms of Coexistence in Vultures: Understanding the Patterns of Vulture Abundance at Carcasses in Masai Mara National Reserve, Kenya. *Condor* 114: 523–531.

Kristan, W. B. and Boarman, W. I. (2007) Effects of anthropogenic developments on common Raven nesting biology in the west Mojave Desert. *Ecol. Appl.* 17: 1703–1713.

Kruuk, H. (1967) Competition for food between vultures in East Africa. *Ardea* 55: 171–193.

Lambertucci, S. A. (2007) Biología y conservación del Cóndor Andino. *Hornero* 22: 149–158.

Lambertucci, S. A. (2010) Size and spatio-temporal variations of the Andean condor *Vultur gryphus* population in north-west Patagonia, Argentina: communal roosts and conservation. *Oryx* 44: 441–447.

Lambertucci, S. A., Alarcón, P., Hiraldo, F., Sanchez-Zapata, J. A., Blanco, G., Donázar, J. A. (2014) Apex scavenger movements call for transboundary conservation policies. *Biol. Conserv.* 170: 145–150.

Lambertucci, S. A., Donazar, J. A., Huertas, A. D., Jiménez, B., Sáez, M., Sanchez-Zapata, J. A. and Hiraldo, F. (2011) Widening the problem of lead poisoning to a South-American top scavenger: Lead concentrations in feathers of wild Andean condors. *Biol. Conserv.* 144: 1464–1471.

Lambertucci, S. A., Speziale, K. L., Rogers, T. E. and Morales, J. M. (2009a) How do roads affect the habitat use of an assemblage of scavenging raptors? *Biodivers. Conserv.* 18: 2063–2074.

Lambertucci, S. A., Trejo, A., Di Martino, S., Sánchez-Zapata, J. A., Donázar, J. A. and Hiraldo, F. (2009b) Spatial and temporal patterns in the diet of the Andean condor: ecological replacement of native fauna by exotic species. *Anim. Conserv.* 12: 338–345.

Monsarrat, S., Benhamou, S., Sarrazin, F., Bessa-Gomes, C., Bouten, W. and Duriez, O. (2013) How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers? *PLoS One* 8: 1–11.

Moreno-Opo, R., Trujillano, A. and Margalida, A. (2016) Behavioural coexistence and feeding efficiency drive niche partitioning at carcasses within the guild of European avian scavengers. *Behavioral Ecology* 27: 1041–1052.

Moreno-Opo, R., Trujillano, A., Arredondo, A., González, L. M. and Margalida, A. (2015) Manipulating size, amount and appearance of food inputs to optimize supplementary feeding programs for European vultures. *Biol. Conserv.* 181: 27–35.

Novaes, W. G. and Cintra, R. (2013) Factors influencing the selection of communal roost sites by the black vulture *Coragyps atratus* (Aves: Cathartidae) in an urban area in central amazon. *Zoologia* 30: 607–614.

Novillo, A. and Ojeda, R. A. (2008) The exotic mammals of Argentina. *Biol. Invasions* 10: 1333–1344.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M. S. and Martínez Abraín, A. (2013) Ecological and evolutionary implications of food subsidies from humans. *Ecol. Lett.* 16: 1501–1514.

Oro, D., Margalida, A., Carrete, M., Heredia, R. and Donázar, J. A. (2008) Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. *PLoS One* 3: e4084.

Paruelo, J. M., Beltran, A., Jobbagy, E., Sala, O. E. and Golluscio, R. A. (1998) The climate of Patagonia: General patterns and controls on biotic processes. *Ecol. Austral* 8: 85–101.

Pianka, E. R. (1973) The structure of lizard communities. *Annu. Rev. Ecol. Systemat.* 4: 53–74.

Pianka, E. R. (1985) *Ecología evolutiva*. Barcelona, Spain: Omega.

Plaza, P. I. and Lambertucci, S. A. (2017) How are garbage dumps impacting vertebrate demography, heath, and conservation? *Global Ecology and Conservation* 12: 9–20.

Prior, K. A. and Weatherhead, P. J. (2004) Turkey vultures foraging at experimental food patches: a test of information transfer at communal roosts. *Behav. Ecol. Sociobiol.* 28: 385–390.

Real, J. (1996) Biases in diet study methods in the Bonelli´s Eagle. *J. Wildl. Manage.* 60: 632–638.

Sánchez, R., Margalida, A., González, L. M. and Oria, J. (2008) Biases in diet sampling methods in the Spanish Imperial Eagle *Aquila adalberti*. *Ornis Fennica* 85: 82–89.

Sazima, I. (2007) Unexpected cleaners: Black Vultures (*Coragyps atratus*) remove debris, ticks, and peck at sores of capybaras (*Hydrochoerus hydrochaeris*), with an overview of tick-removing birds in Brazil. *Rev. Bras. Ornitol.* 15: 417–426.

Selva, N. and Fortuna, M. a (2007) The nested structure of a scavenger community. *Proc. Biol. Sci.* 274: 1101–1108.

Shepard, E. L. C. and Lambertucci, S. A. (2013) From daily movements to population distributions: weather affects competitive ability in a guild of soaring birds. *J. R. Soc. Interface* 10: 20130612.

Speziale, K. L., Lambertucci, S. A., Carrete, M. and Tella, J. L. (2012) Dealing with non-native species: what makes the difference in South America? *Biol. Invasions* 14: 1609–1621.

Speziale, K. L., Lambertucci, S. A. and Olsson, O. (2008) Disturbance from roads negatively affects Andean condor habitat use. *Biol. Conserv.* 141: 1765–1772.

Steigerwald, E. C., Igual, J.-M., Payo-Payo, A. and Tavecchia, G. (2015) Effects of decreased anthropogenic food availability on an opportunistic gull: evidence for a size-mediated response in breeding females. *Ibis* 157: 439–448.

Stolen, E. D. (1996) Black and turkey vulture interactions with bald eagles in florida. *Florida Field Nat.* 24: 43–45.

Stolen, E. D. (2000) Foraging behavior of vultures in central Florida. *Florida Field Nat.* 28: 173–181.

Thomaides, C., Valdez, R., Reid, W. H. and Raitt, R. J. (1989) Food habits of turkey vultures in West Texas. *J. Raptor Res.* 23: 42–44.

Tonni, E. P. and Noriega, J. I. (1988) Los cóndores (Ciconiiformes, Vulturidae) de la Región Pampeana de la Argentina durante el cenozoico tardío: distribución, interacciones y extinciones. *Ameghiniana* 35: 141–150.

Wallace, M. P. and Temple, S. A. (1987) Competitive interactions within and between species in a guild of avian scavengers. *Auk* 104: 290–295.

Wilmers, C. C., Stahler, D. R., Crabtree, R. L., Smith, D. W. and Getz, W. M. (2003) Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. *Ecol. Lett.* 6: 996–1003.

Wilson, E. E. and Wolkovich, E. M. (2011) Scavenging: how carnivores and carrion structure communities. *Trends Ecol. Evol.* 26: 129–135.

FERNANDO BALLEJO*, SERGIO A. LAMBERTUCCI
Grupo de Biología de la Conservación, Laboratorio Ecotono, INIBIOMA (CONICET,
   Universidad Nacional del Comahue), Bariloche, Argentina.

ANA TREJO
Department of Zoology, Universidad Nacional del Comahue, Bariloche, Argentina.

LUCIANO J. M. DE SANTIS
Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales y Museo, Universidad
   Nacional de La Plata. La Plata, Buenos Aires, Argentina.

*Author for correspondence; email: fernandoballejo@hotmail.com