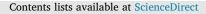
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Nature's clean-up crew: Quantifying ecosystem services offered by a migratory avian scavenger on a continental scale



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ABSTRACT

Despite its importance for ecosystem and human health, the cleaning service provided by scavenging birds is frequently disregarded. We evaluated this ecosystem service provided by a migratory species at a continental scale, estimating the amount of annual organic material removal, and the cost of artificially replacing the service. Road surveys conducted between 2005 and 2011, indicated an abundance of Turkey Vultures (*Cathartes aura*) of nearly 9,000 birds along 27,658 km (22,127 km²), suggesting that the total global population could approximate 13 million birds. The calculated individual food intake (252 g/day) suggests that the surveyed population remove 1,000 tons of organic material per year –a monetized service of more than 500,000 USD, that could reach 700 million USD per year for the global population. Movement data from 22 tagged birds showed that the ecosystem service is maximized at the breeding and wintering areas, where Turkey Vultures spend most of the year (74–92% of time). The huge amount of organic material removed by Turkey Vultures at a continental scale, and the economic relevance of their service, highlight the importance of widespread and abundant populations of scavenging birds and their significant role in protecting the health of the environment and human wellbeing.

1. Introduction

Organic material composes 46% of the global urban solid waste, with proved detrimental effects on the health of both the environment and human populations (Hoornweg and Bhada-Tata, 2012). Currently, one-third (1.3 billion tons) of the edible food produced worldwide for human consumption is lost or wasted every year, and constitutes 10-25% of the meat production and 30-50% of the initial catching of fish and seafood (FAO, 2011). Organic waste is generated at each step in the food processing chain, from the rearing of animals to slaughter, processing, and commercialization. In the USA alone, the death of cattle and calves during the rearing stage was close to 3.9 million animals in 2015, not only young animals but 1.7 million of them weighting over 227 kg (500 lb) (USDA, 2015), and despite most (91%) of the industrial food waste generated during slaughter and processing in the meat sector in USA is being used as by-product (U.S. Environmental Protection Agency, 2012) much of the final production of food worldwide is finally disposed of (FAO, 2011). All that organic material remaining in the environment, has several consequences through the increase of human-wildlife conflicts and of disease transmission (Ortiz and Smith, 1994; Ogada et al., 2012a,b). In this context, the regulating contribution (Díaz et al., 2018) provided by scavengers in removing organic waste has a high global impact, both in sanitary and economical terms (Şekercioğlu, 2006; Markandya et al., 2008; Dupont et al., 2012; Morales-Reyes et al., 2015).

Summoning and sustaining public support for ecosystem services can be challenging, particularly when the organisms offering them lack charisma, and when there is a combination –actual or perceived– of detrimental and beneficial contributions of nature to people (DeVault et al., 2016; Şekercioğlu et al., 2016). The public perception of the ecological value of these species and the ecosystem services they provide is strongly influenced by cultural and socioeconomic aspects, education frameworks and human-wildlife conflicts born from some real damages caused by the target species (Lowney, 1999). Moreover, a principal barrier to building a compelling argument for ecosystem services is that it is often difficult to simplify and quantify the magnitude of services offered by the species in question (Şekercioğlu et al., 2016). In many cases, avian communities have been linked to the important ecosystem service of agricultural pest control through predatory behavior (Whelan et al., 2016). Unfortunately, the role that birds play

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as scavengers of organic material in both human-dominated and natural landscapes, and as a consequence in reducing populations of potential disease-causing organisms, is less well understood and appreciated (Putman, 1983; DeVault et al., 2016; Şekercioğlu et al., 2016).

Avian scavengers including vultures reduce both organic humancreated waste –agricultural and otherwise–, and the carcasses of both livestock and wildlife. In many ecosystems vultures, as obligate scavengers, are the most functionally significant members of vertebrate scavenging guilds (DeVault et al., 2003; Whelan et al., 2008). In their absence organic material either accumulates in the environment where it decays and rots (Hill et al., 2018), and/or favors the growth of populations of mammalian facultative scavengers including rats and feral dogs, that, in turn, can increase disease transmission to humans, their livestock, and other fauna (Markandya et al., 2008; Ogada et al., 2012b). In addition to reducing the availability of carcasses and organic material overall, vulture scavenging may also control the spread of infectious diseases when the birds decrease, in their digestive system, some of the pathogens of the rotten organic material (Houston and Cooper, 1975; Roggenbuck et al., 2014).

The ongoing massive production of human organic waste intensifies the association between vultures and humans (Campbell, 2009; Gangoso et al., 2013; Novaes and Cintra, 2015; Tauler-Ametller et al., 2017) which, in turn, increases the functional significance of these scavengers and their contribution to people in human-dominated landscapes. All of this combines to make vultures key components of the ecosystem, not only for maintaining the health and balance of ecosystems but also for protecting the health of human populations, helping to remediate one of the main environmental problems that humans produce.

Ecosystem services are most significant when the organisms providing them are widespread and abundant (Gaston et al., 2018). In the New World, the Turkey Vulture (*Cathartes aura*) is an obligate scavenger able to find carcasses even in areas with low visibility, making use of its developed smell sense (Houston, 1986; Platt et al., 2015). This species has a huge range across more than 37 million km², from 53°N across south-central Canada in North America to 55°S at the southern tip of South America (Ferguson-Lees and Christie, 2001). Although no reliable estimates of their total abundance exist, their global population is estimated to be of several million individuals (Ferguson-Lees and Christie, 2001). Moreover, many individuals perform annual long-distance migrations (Dodge et al., 2014; Graña Grilli et al., 2017), bringing their ecosystem services seasonally to areas without resident breeding populations.

Here, we aim to quantify and raise awareness of the ecosystem service provided by Turkey Vultures estimating the total amount of organic material they remove annually from areas surveyed across their continental distribution and considering also their seasonal movements. The lack of reliable data on the global population of Turkey Vultures, and of the likely cost of removal of organic waste from the environment in such a variable geographic area in terms of environmental characteristics, proximity to treatment points, and magnitude of the human economy, could be limiting factors in our approximation. However, we use a series of conservative decisions regarding the available information, to provide an initial insight into the size and economic value of the contribution to people of one common and widespread avian scavenger throughout its global distribution. On one hand, we use a population approach, using road-side counts at a continental scale to estimate the annual mass of food consumption by these populations and the associated cost derived from the artificial removal of the same mass of organic material. On the other hand, to evaluate the scope of the service at an individual level we used satellite tracks of birds from migratory populations to identify the timing of the service provided in different areas and the range of the service provided by individual birds during their residence periods.

2. Methods

2.1. Population surveys areas, roads and dates

We surveyed vultures along 27,658 km of primary and secondary roads in 2005 through 2011, throughout regions of Canada and the United States in North America; throughout Costa Rica and eastern Panama in Central America, and in regions of Argentina, Chile, Uruguay, and Venezuela in South America (Fig. 1, Table 1). Counts were completed by two experienced observers that drove and counted at the same time, one of whom was the same in all the surveys. In keeping with other road counts (Denes et al., 2017; Tryjanowski and Morelli, 2018), we (1) limited counts to two times of the year: breeding season (summer) and non-breeding season (winter), when vultures are not migrating in the survey area, so as to identify regional changes in abundance related to the migratory habits. The only exceptions to this scheme were the southernmost (roads 1 and 2, Table 1) and northernmost (roads 19, 20 and 21, Table 1) survey regions, where surveys were not conducted in winter, as all individuals breeding in those regions migrate out of the areas (Bildstein, unpublished data). We also (2) limited the count to times of the day when vultures were likely to be foraging rather than travelling to and from nocturnal roosts (i.e., 09.30 through 15.30 h) (Kirk and Currall, 1994), (3) surveyed 100-300 km each day, (4) recorded the latitude and longitude at the start and end of each survey, (5) traveled at speeds of 40-70 km/h, (6) limited our counts to rainless periods, or periods interrupted by rains of fewer than five minutes, (7) recorded the locations of Turkey Vultures seen to the nearest tenth of a kilometer, (8) recorded all individuals seen within 400 m of either side of the road, including both perched and flying individuals, and (9) stopped when needed to identify distant individuals to species, as well as to count the number of individuals in large flocks, but when stopped, included only those birds initially spotted and not any new birds sighted after stopping.

As in similar studies, data obtained by the single-visit method of the road-side counts were used to estimate the abundance of Turkey Vultures in different areas of their distribution (e.g. Fuller and Mosher, 1987; Donázar et al., 1993; Sanchez-Zapata et al., 2003; Prakash et al., 2017). To increase the roadside coverage of the study, densities of Turkey Vultures were calculated from published data for road-side counts (which used a similar method to ours) in the Cerrado and Pantanal of Brazil (Denes et al., 2017) and in Cuba (Tryjanowski and Morelli, 2018). In all cases, we used the limit distance of 400 m to each side of the road as the maximum distance for the counted birds to estimate their density. We then used the total number of Turkey Vultures counted along each survey, the length of the road and the 0.8 km width to calculate the densities of vultures per km² for each surveyed road, as we do not have exact distances to each individual. We should note that previous information suggest that the presence of Turkey Vultures is not influenced by primary or secondary roads (Barbar et al., 2015), therefore, our methodology would not overestimate the density of the species by sampling particularly dense areas.

Three subspecies of Turkey Vultures (*C. aura meridionalis, aura* and *ruficollis*), and the Lesser Yellow-headed Vulture (*C. burrovianus*) occurred in parts of the survey areas –Venezuela, Panama and Costa Rica–(Stiles and Skutch, 1989; Ridgely and Gwynne, 1992). Although we did not attempt to characterize all of the *Cathartes* vultures we counted to species or subspecies, the overwhelming majority (i.e., > 95%) of those that we were able to identify belonged to one of the three subspecies of Turkey Vultures and not to Lesser Yellow-headed Vultures, and for the purposes of our analyses, we considered all *Cathartes* counted to have been Turkey Vultures.

2.2. Timing and geography of movement patterns

We deployed GPS units on 22 birds from four populations for from 6 to 77 months each, to identify the timing and geography of movements

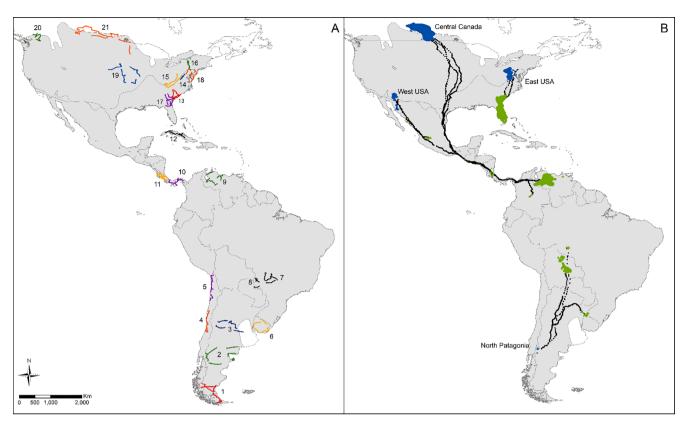


Fig. 1. (A) Detail of the road surveys carried out to determine the density of Turkey Vultures (*Cathartes aura*) in summer. Roads 7, 8 modified from Denes et al. (2015) and 12 modified from Tryjanowski and Morelli (2018). (B) Location of the breeding (blue) and wintering (green) sites of the tagged populations with their connecting migratory journeys. Grey shows the published distribution of Turkey Vultures (BirdLife International and Handbook of the Birds of the World, 2016).

Table 1

Detail of Turkey Vultures (*Cathartes aura*) road censuses and estimated daily food intake (DFI) per square kilometer during each season, and average annual food intake (AAFI) per square kilometer for each surveyed site.

						Breedir	ng season			Non-Breedin	g season	
Region	Country	Area	Road	Longitude (km)	Area (km ²)	Count	Density (birds/ km²)	DFI (kg/ day·km²)	Count	Density (birds/ km²)	DFI (kg/ day·km²)	AAFI (kg∕ year∙km²)
South America	Argentina	South Patagonia	1	1,604	1,283	4	0.003	8·10 ⁻⁴	-	-	-	0.156
		North Patagonia	2	1,824	1,459	248	0.170	0.043	-	-	-	8.372
		Central	3	1,447	1,158	106	0.092	0.024	0	0	0	4.380
	Chile	Central	4	1,151	921	211	0.229	0.059	123	0.134	0.034	16.972
		North	5	976	781	1,428	1.828	0.470	1,405	1.799	0.462	170.090
	Uruguay		6	1,171	937	348	0.371	0.095	87	0.093	0.024	21.718
	Brazil ^a	Cerrado	7	1,400	1,120	161	0.144	0.037	248	0.221	0.057	17.155
		Pantanal	8	340	272	30	0.110	0.028	107	0.393	0.101	23.542
	Venezuela		9	1,383	1,106	531	0.480	0.130	2,504	2.264	0.613	135.598
Central America	Panama		10	962	770	569	0.738	0.200	1,417	1.840	0.499	127.568
& Caribe	Costa Rica		11	1,562	1,250	1,008	0.806	0.218	913	0.730	0.198	75.920
	Cuba ^b		12	2,384	1,907	1,231	0.646	0.175	-	-	-	63.875
North America	USA	East	13	964	771	194	0.252	0.068	712	0.923	0.250	58.035
			14	409	327	125	0.382	0.103	66	0.202	0.055	28.835
			15	1,542	1,234	487	0.395	0.107	103	0.083	0.022	23.542
			16	481	385	35	0.091	0.025	0	0	0	4.563
			17	1,326	1,061	246	0.232	0.063	840	0.792	0.215	50.735
			18	1,018	814	986	1.211	0.328	452	0.555	0.150	87.235
		Central	19	1,901	1,521	620	0.408	0.093	-	-	-	17.159
	Canada		20	1,074	859	44	0.051	0.012	-	-	-	1.754
	North USA/ South Canada		21	2,739	2,191	51	0.023	0.005	-	-	-	0.731
TOTAL				27,658	22,127	8,663	0.392	0.109	8,977	0.406	0.179	44.664

^a Denes et al. (2017).

^b Tryjanowski and Morelli (2018).

of migratory populations in the following regions: central Canada (n = 7; 53°0′16″N, 106°18′47″W); eastern USA (n = 2; 40°38′20″N, 76°1′6″W); western USA (n = 9; 33°23′20″N, 112°40′59″W); and north Patagonia (n = 4; 41°11′14″S, 71°8′40″W). All tagged birds were trapped using baited monofilament loop traps (adapted from padded leg-hold trap, Bloom et al., 2007). Individuals were fitted either with PTT-100 model, from Microwave Telemetry; Model 40 GPS, from Northstar Science and Technology; or CTT-1000-BT3, from Cellular Tracking Technology, that collected GPS locations every 0:15, 1 or 3 h daily between 07:00 and 00:00 (see more details in Graña Grilli et al., 2017).

We defined the migratory journeys as occurring from the start of one-way movements on consecutive days greater than 50 km (Graña Grilli et al., 2017). We then calculated the time the birds remained at the breeding and wintering sites and on the outbound and returning migrations. We also identified the time the birds remained at an specific site along the migratory path by counting the stopover days, which were identified following Graña Grilli et al. (2017) as the days during migrations when the displacement was shorter than 20 km. To identify the range where Turkey Vultures provide their ecosystem service during residence periods, we estimated the home range of each bird in the breeding and wintering sites by calculating the utilization distribution estimation (99% isopleth) using the package *adehabitatHR* (Calenge, 2006) for R software (Core and Team, 2014).

2.3. Annual food consumption and associated cost

We used estimates of Turkey Vulture populations for each region and the individual daily food intake for vultures in each region to calculate the total annual food consumption for each surveyed population. Following Bozinovic and Medel (1988), we estimated the daily food intake as: FI (g/day) = FMR (KJ/day)/(6.65 KJ/g·76.9 %), where 6.65 KJ is the caloric content per gram of a small mammal (Hamilton, 1985), 76.9 % is the assumed mean assimilation efficiency, and FMR is the field metabolic rate, calculated as 10.9 M^{0.64}, where M the body mass of Turkey Vultures (Bozinovic and Medel, 1988).

We calculated the daily food intake for each Turkey Vulture subspecies from body mass data we collected when trapping them -C. a. meridionalis (Canada and West USA), C. a. septentrionalis (East USA) and C. a. jota (North Patagonia)-. Using the estimation of the population size at each site and the individual daily food intake for the corresponding subspecies we calculated the minimum total annual food consumption by Turkey Vultures at each surveyed area. Subspecies were assigned as C. a. jota for roads 1-8, C. a. septentrionalis for roads 9-18, and C. a. meridionalis for roads 19-21. Because the total food consumption varied along routes where the density of birds changes seasonally due to migration, for those localities where counts were conducted in both breeding and non-breeding seasons, annual food intake was calculated as the averaged amount estimated for each season. In regions where a non-breeding survey was not conducted because populations evacuated the region (roads 1, 2, 19, 20 and 21, Table 1), the annual food intake was considered to be that of the breeding season. There, the duration of the breeding season was considered to be the average days of the breeding season of the birds tracked in North Patagonia for roads 1 and 2, in Eastern USA for road 19, and in Central Canada for roads 20 and 21 (Table 2). For localities in which surveys were not conducted in the non-breeding season, but the population is known to occur year-round (road 12, Table 1), we estimated annual food consumption based on breeding season figures.

To estimate the percentage of the total distribution of the Turkey Vulture in which this ecosystem service benefits the most people, we overlapped the distribution of Turkey Vultures (BirdLife International and Handbook of the Birds of the World, 2016) with maps of human density (Center for International Earth Science Information Nerwork – CIESIN – Columbia University, 2017), cow, sheep and goat, per km² (Robinson et al., 2014). Also, by determining the density of people

inside the area of censuses, we estimated the number of people that benefited from the service provided by the minimum density of Turkey Vultures determined by our census.

To obtain an estimate of the annual cost of artificial removal of carcasses we used published data from Spain, where the outbreak of bovine spongiform encephalopathy led to the documented collection of carcasses from farms and the incineration of livestock in plants. Such a strategy has never been carried out in any country in the distribution of Turkey Vultures, and the data from Spain constitute the only numbers available for the costs of collection and treatment of carcasses at a large geographic scale, and we use them to estimate cost associated with such a public removal that countries should afford if needed. The annual biomass of dead cattle in Spain in 2012 was 96,613,484 kg, the removal of which cost 50 million USD (Morales-Reyes et al., 2015). Based on these numbers, which constitute the only one reliable estimation of the cost waste removal, we estimated, the economic cost of the artificial removal of the amount of organic material removed by Turkey Vultures in our surveyed area.

3. Results

3.1. Population surveys

The mean number of vultures we counted during the breeding and non-breeding seasons was 8,820 (including our census and the census obtained from the bibliography for Brazil and Cuba, which totaled 8,663 birds during the breeding season and 8,977 during the nonbreeding season) during the breeding and non-breeding seasons along 27,658 km surveyed in different areas of the American continent (Fig. 1a). Our results demonstrate lower densities of Turkey Vultures at higher latitudes –Southern Patagonia (road 1) and Northern USA and Canada (roads 20, 21)– with higher densities at some of the lower temperate latitudes –Northern Chile (road 4) and Eastern USA (road 18)– (Table 1; Fig. 1a). Seasonal variations in densities also indicate the desertion from higher latitudes after the breeding season as well as the arrival at lower latitudes of migratory birds that spent the non-breeding season there.

3.2. Timing and geography of movement patterns

The study at the individual level based on satellite tracks indicated that Turkey Vultures spend more time at their breeding and wintering sites (i.e.: between 74 and 92% of days annually) than on their migrations (Table 2), with both spring and autumn migrations generally taking fewer than three months per year in total. Migrations were longer during the outbound than during the returning migration, with generally none or a few stopover days (Table 2).

The area covered during residence periods by the birds of all the populations pooled was $88,994 \text{ km}^2$, being larger at the wintering $(79,505 \text{ km}^2)$ than at the breeding sites $(9,489 \text{ km}^2)$. However, there was a high variability in the median size of the home range for the breeding and wintering periods for all the populations (Table 2).

3.3. Total annual food consumption and associated cost

The average daily food intake of Turkey Vultures was $252.2 \text{ g} (\pm 21.7 \text{ g})$ (Table 3). Therefore, considering the number of birds counted during each season and the daily food intake estimated for each subspecies, total annual food intake for the surveyed areas –and therefore the amount of material removed from the environment–by Turkey Vultures was estimated to be 988,280 kg in an area of 22,127 km², or approximately 0.12 kg per km² per day (Table 1).

Overall human density averaged 155 people per km^2 in our surveyed areas (0–38,221). The distribution of the Turkey Vulture overlaps 87% with a human density of at least one person per km^2 , and 93% with a livestock density (either cow, sheep or goat) of at least one head per

Table 2

Duration of migration, stopovers, and of the breeding and wintering periods and their home-range size for five populations of Turkey Vultures (*Cathartes aura*). Duration is presented as mean \pm SD; Area is presented as median \pm SD. Sample size in squared brackets.

	Duration (days)							Area (km ²)		
Population	Breeding site	Wintering site	Outbound migration	Returning migration	Stopovers Out. mig.	Stopovers Ret. mig.	Breeding site	Wintering site		
Canada	146.2 (± 14.1) [6]	124.0 (± 17.7) [7]	51.0 (± 10.6) [7]	41.7 (± 9.2) [7]	6.5 (± 4.7) [7]	5.9 (± 2.7) [7]	931 (± 17,750) [6]	4,557 (± 37,568) [6]		
Eastern USA	184.5 [1]	140.1 (±11.1) [2]	18.3 (± 2.4) [2]	9.8 (± 0.2) [2]	$7.1 (\pm 0.2)$	1.0 (± 1.5) [2]	5,447 [1]	71,071 (± 38,231) [2]		
Western USA	197.8 (± 9.9) [8]	130.0 (± 12.5) [9]	18.8 (± 7.7) [9]	15.8 (± 7.2) [9]	1.1 (± 1.6) [9]	1.9 (± 4.9) [9]	2,297 (± 3,494) [8]	283 (±1,239) [9]		
North Patagonia	191.5 (± 9.4) [4]	137.9 (± 4.0) [4]	22.7 (± 6.0) [4]	17.2 (± 5.4) [4]	2.3 (± 1.2) [4]	2.5 (± 1.2) [4]	814 (± 695) [4]	3,594 (± 5,279) [4]		

Table 3

Individual daily food intake of the three studied subspecies of Turkey Vultures. Mass is given as mean \pm SD and sample size in squared brackets. FMR: field metabolic rate, FI: food intake.

	C. a. meridionalis	C. a. septentrionalis	C. a. jota
Mass (g)	1,486.4 (± 169.3)	1,940.7 (± 169.5)	1,788.6 (± 82.7)
	[36]	[70]	[7]
FMR (KJ/day)	1,168.4	1,385.9	1,315.3
FI (g/day)	228.5	271.0	257.2

km², and 48% of a minimum density of at least 10 heads per km². Moreover, the 82% and 46% of the total distribution of the species overlap with the simultaneous presence of people and livestock in densities of at least 1 or 10 heads per km², respectively.

Based on the cost of artificial removal of dead cattle in Spain, we estimate that it would cost 511,461 USD per year to remove the organic material consumed by Turkey Vultures from the surveyed areas. Assuming that the average bird density calculated from our surveys is representative of that in the entire distribution of the species, this would mean a total estimated population of Turkey Vultures of 13,154,065 individuals, which would remove 1,473,911,511 kg of organic material annually, representing an annual cost of 762,787,682 USD, assuming human removal of the equivalent amount of organic material.

4. Discussion

We estimated the potential value of the ecosystem service provided by a single common and widespread obligate avian scavenger through the entire Americas. Just in the small portion of the distribution of Turkey Vultures surveyed –only 0.07% of its estimated entire distribution–, this species is able to remove nearly 1,000 tons of organic material annually, which can be translated into monetary terms in more than 500,000 USD per year. In addition, only 22 satellite-tracked individuals showed that each bird provides its service in an area that collectively covers nearly 90,000 km². Over 90% of the distribution of the species occur in areas where it can provide beneficial contributions to people, removing the carcasses of both livestock and wildlife, and also other organic waste, whose permanence in the environment can be of major concern of human health mainly because of the risk for zoonotic diseases (Markandya et al., 2008; Ogada et al., 2012a).

The figure of more than \$700 million USD for the annual cost of artificial removal of organic waste from throughout the Turkey Vultures' range is a gross approximation, based on the cost of the artificial removal from Spain, and likely will differ among locations within the distribution of the species. Spain is a high-income country, in which costs associated with carcass removal are likely to be higher than in lower-income economies, as the cost of collection and incineration of solid waste in high-income economies are 85–250 and 70–200 USD/ton

respectively, whereas in lower-middle-income countries those figures drop to 30–75 and 40–100 USD/ton for collection and incineration, respectively (Hoornweg and Bhada-Tata, 2012). As 38% of the global distribution of the Turkey Vulture falls within high-income countries, whereas 55% falls within upper-middle-income countries, and 7% is in lower-middle-income countries, our estimate of the human cost of carcass removal may be overestimated. Given the assumptions made in our calculations and the broad range of the costs used, the figures given are best considered as indicative. Further studies would be useful to estimate the real cost of replacing the ecosystem service at smaller local scales. However, our results remain useful in providing an estimate of the economic impact of the lack of obligate avian scavengers in an area if a country were to use the methods (and associated costs) of a developed country such as Spain.

Because the distribution of Turkey Vultures can show temporal changes according to food availability (Donázar et al., 1993), our roadcounts may have underestimated its population. False zeros created by both imperfect detection and temporary absence from the surveyed areas, may have reduced our density estimations from the real abundance in the areas surveyed (Denes et al., 2015). Therefore, the estimated ecosystem service provided by this species is likely to be underestimated in some of the surveyed areas. Nonetheless, we must also note that the diet of Turkey Vultures includes carcasses of wild animals, and even small birds, reptiles, and arthropods (Ballejo et al., 2018), in addition to large carcasses of domestic animals. That would, reduce the total amount of large organic material removed from that estimated here, but cannot be quantified due to a lack of data of wild animals mortality and carcass availability. Despite these limitations, the approach used here gave us an estimation of a possible population size for the species, a gross estimation of its organic material removal throughout the species' range, as well as identifying differences in abundance in different regions and seasons.

Our results indicate high variability in vulture density, with the lowest densities occurring at higher latitudes. Despite our surveys covering a big area of the continent, large areas remain without data. The heterogeneous distribution of Turkey Vultures leads to an unequal amount of organic material removal throughout the continent. Heterogeneity is also temporal due to the migratory movements of many populations. In this sense, the magnitude of the service provided is especially important in the breeding and wintering sites, where Turkey Vultures spend most of the time, as well as in those localities with year-round resident populations, and reduced to only a few days during stopovers in the migratory journeys. However, even a small individual effect along the migratory journey can constitute a real sweeping system when thousands of birds pass in a short time through an area, as takes place in the Mesoamerican Land Corridor (Bildstein, 2004). Moreover, other species of the scavenger guild also contribute to the phenomenon of organic material removal and maintain the service when Turkey Vultures are absent or less abundant in a site.

In both Asia and Africa population declines in avian scavengers

have been shown to increase the decomposition time of carcasses and the attendance of facultative scavengers, phenomena that may raise serious consequences for public health (Markandya et al., 2008; Ogada et al., 2012b). In southern Asia where the abundance of scavenging birds was declined catastrophically, the increase in disease transmission through both direct pathogen propagation and transmission from facultative scavengers (e.g. dogs, rats, hyenas) has markedly impacted human populations (Markandya et al., 2008). The replacement of the service provided by Turkey Vultures would involve an high economic cost for the removal of organic material and, possibly, the remediation of the effects of carbon emanations caused by a system including transport and incineration of carcasses (Dupont et al., 2012; Morales-Reves et al., 2015). However, more important than those economic costs, could be the fundamental importance of the cleaning service in the prevention of disease transmission if proved, and proliferation of facultative scavengers, which can also be predators of both cattle and wildlife, and act as disease vectors too (Markandya et al., 2008; Ogada et al., 2012a; O'Bryan et al., 2019).

In spite of all the benefits provided by scavenging birds, this avian guild, typically, is not held in high esteem by the general public (Margalida et al., 2014; Cailly Arnulphi et al., 2017; but see Santangeli et al., 2016). Indeed, the aversion generated by the feeding habits of these species sometimes lowers their popularity with people, including farmers who often consider them as frequent predators (Cailly Arnulphi et al., 2017; Morales-Reyes et al., 2017). All that, added to some cases of damages to structures or eventual attacks to vulnerable livestock, mainly by the commonly confused Black Vulture (Coragyps atratus) (Avery and Cummings, 2004), lead in many instances to their active persecution via poisoning and shooting (Boshoff and Vernon, 1980; Lowney, 1999; Donázar et al., 2016; Cailly Arnulphi et al., 2017). The cleaning services provided by vultures not only is not valued as an important ecosystem service, but ironically, it heightens their vulnerability to ingesting potentially harmful non-digestible materials (Torres-Mura et al., 2015; Augé, 2017), as well as to toxic veterinary drugs (Green et al., 2004; Blanco et al., 2017) and other agricultural toxins (Richards, 2011), and to active persecution (Ogada et al., 2012a; Santangeli et al., 2016).

Because of such persecution most vulture species are now endangered globally (Buechley and Şekercioğlu, 2016). Although Turkey Vultures remain widespread and abundant, serious population persecution and declines have occurred in the New World for the two species of condors (Walters et al., 2010; Alarcón and Lambertucci, 2018). Moreover, there is growing evidence of direct and indirect persecution of all the scavenging birds throughout the Americas (Lowney, 1999; Pavezi and Estades, 2016). Where persecution continues to grow in the New World, and where such persecution has a detrimental effect on the sizes of populations of Turkey Vultures and other avian scavengers, the results presented above suggest that the impacts would not be limited to the avian scavengers alone, but also to the ecosystems they inhabit, the services they provide and the human populations with which they cooccur.

5. Conclusion

The Turkey Vultures' ability to find and consume carrion (Houston, 1986; Platt et al., 2015) makes them –and other scavenger species sharing those characteristics– key components of the nature contributions to people (Díaz et al., 2018). Further qualities that contribute to the species cleaning efficacy are their abundance, wide distribution, and their overlap with humans. The magnitude of the ecosystem service increases if we consider that the service provided by Turkey Vultures is reinforced by the simultaneous action of other species of the scavenging bird guild, which face the same threats. This situation becomes even more noteworthy when we consider that Turkey Vultures occur in many developing countries where, even when the treatment costs may be lower than in high-income economies, successfully dealing with the

cost of replacing the ecosystem service provided by avian scavengers would be challenging and have a proportionally higher impact on their economies.

Biodiversity conservation efforts may focus on so-called flagship species, in part because they are more likely to receive significant public support (Caro and O'doherty, 1999; Caro, 2010). But in many instances ecosystem services provided by less charismatic species can be substantial and even critical (Christie et al., 2016; Sekercioğlu et al., 2016; Senzaki et al., 2017). In this context, it is important to take actions to clearly show the beneficial contributions they provide while taking local knowledge and experiences as a basis, in order to increase the society's awareness so as to better preserve vultures. The same threats faced by some scavenging birds can be experienced by the whole guild, and a decrease of its ecosystem service can lead to an increase in carrion availability in the environment leading to higher disease transmission (Houston and Cooper, 1975), and/or an increase in the populations of mesoscavengers, with further conflicts with humans and wildlife (Ogada et al., 2012b; O'Bryan et al., 2019). Therefore, from a utilitarian perspective, this is particularly relevant for widespread and abundant scavenger species, in order to maintain and enhance their ecosystem service efficiency and through it, retain both functionally healthy environments and a good quality of life for human populations.

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References

- Alarcón, P.A., Lambertucci, S.A., 2018. Pesticides thwart condor conservation. Science 360, 612.
- Augé, A.A., 2017. Anthropogenic debris in the diet of turkey vultures (*Cathartes aura*) in a remote and low-populated South Atlantic island. Polar Biol. 40, 799–805.
- Avery, M.L., Cummings, J.L., 2004. Livestock depredations by black vultures and golden eagles. Sheep Goat Res. J. 19, 58–63.
- Ballejo, F., Lambertucci, S.A., Trejo, A., De Sanctis, L.M.J., 2018. Trophic niche overlap among scavengers in Patagonia supports the condor-vulture competition hypothesis. Bird Conserv International:1–13.
- Barbar, F., Werenkraut, V., Morales, J.M., Lambertucci, S.A., 2015. Emerging ecosystems change the spatial distribution of top carnivores even in poorly populated areas. PLoS ONE 10, e0118851.
- Bildstein, K.L., 2004. Raptor migration in the Neotropics: patterns, processes, and consequences. Ornitol. Neotrop. 15, 83–99.
- Bird Life International and Handbook of the Birds of the World, 2016. Cathartes aura. The IUCN Red List of Threatened Species. Version 3, May 2017. https://www.iucnredlist.org. Downloaded on 18 August 2018.
- Blanco, G., Junza, A., Barrón, D., 2017. Food safety in scavenger conservation: diet-associated exposure to livestock pharmaceuticals and opportunist mycoses in threatened Cinereous and Egyptian vultures. Ecotoxicol. Environ. Saf. 135, 292–301.
- Bloom, P., Calrk, W., Kidd, J., 2007. Capture techniques. In: Bird, D., Bildstein, K. (Eds.), Raptor Research Techniques and Management. Hancock House Publishers Ltd, Canada, pp. 193–220.
- Boshoff, A.F., Vernon, C.J., 1980. The past and present distribution and status of the Cape Vulture in the Cape Province. Ostrich 51, 230–250.
- Bozinovic, F., Medel, R.G., 1988. Body size, energetic and foraging mode of raptors in central Chile. Oecologia 75, 456–458.
- Buechley, E.R., Şekercioğlu, Ç.H., 2016. The avian scavenger crisis: looming extinctions, trophic cascades, and loss of critical ecosystem functions. Biol. Conserv. 198, 220–228
- Cailly Arnulphi, V.B., Lambertucci, S.A., Borghi, C.E., 2017. Education can improve the negative perception of a threatened long-lived scavenging bird, the Andean condor. PLoS ONE 12, e0185278.
- Calenge, C., 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516–519.
- Campbell, M., 2009. Factors for the presence of avian scavengers in Accra and Kumasi, Ghana. Area 41, 341–349.
- Caro, T., 2010. Conservation by Proxy: Indicator, Umbrella, Keystone, Flagship, and Other Surrogate Species. Island Press, Washington, DC.
- Caro, T.M., O'doherty, G., 1999. On the use of surrogate species in conservation biology. Conserv. Biol. 13, 805–814.

Center for International Earth Science Information Nerwork – CIESIN – Columbia University. 2017. Gridded Population of the World, Version 4 (GPWv4): Population Density Adjusted to March 2015 Revision UN WPP Country Totals, Revision 10. Available from https://doi.org/10.7927/H49884ZR (accessed October 21, 2018).

Christie, K.S., Gilbert, S.L., Brown, C.L., Hatfield, M., Hanson, L., 2016. Unmanned aircraft systems in wildlife research: current and future applications of a transformative technology. Front. Ecol. Environ. 14, 241–251.

Denes, F.V., Silveira, L.F., Beissinger, S.R., 2015. Estimating abundance of unmarked animal populations: accounting for imperfect detection and other sources of zero inflation. Methods Ecol. Evol. 6, 543–556.

Denes, F.V., Solymos, P., Lele, S., Silveira, L.F., Beissinger, S.R., 2017. Biome-scale signatures of land-use change on raptor abundance: insights from single-visit detectionbased models. J. Appl. Ecol. 54, 1268–1278.

- DeVault, T.L., Beasley, J.C., Olson, Z.H., Moleón, M., Carrete, M., Margalida, A., Sánchez-Zapata, J.A., 2016. Ecosystem services provided by avian scavengers. In: Şekercioğlu, Ç.H., Wenny, D.G., Whelan, C.J. (Eds.), Why Birds Matter: Avian Ecological Function and Ecosystem Services. University of Chicago Press, Chicago, IL, pp. 235–270.
- DeVault, T.L., Rhodes Jr, O.E., Shivik, J.A., 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102, 225–234.
- Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M., Baste, I.A., Brauman, K.A., 2018. Assessing nature's contributions to people. Science 359, 270–272.
- Dodge, S., et al., 2014. Environmental drivers of variability in the movement ecology. Philos. Trans. R. Soc. Lon. B 369, 20130195.
- Donázar, J.A., Ceballos, O., Travaini, A., Hiraldo, F., 1993. Roadside raptor surveys in the Argentinean Patagonia. J. Rapt. Res. 27, 106–110.
- Donázar, J.A., Cortés-Avizanda, A., Fargallo, J.A., Margalida, A., Moleón, M., Morales-Reyes, Z., Moreno-Opo, R., Pérez-García, J.M., Sánchez-Zapata, J.A., Zuberogoitia, I., 2016. Roles of raptors in a changing world: from flagships to providers of key ecosystem services. Ardeola 63, 181–234.
- Dupont, H., Mihoub, J.-B., Bobbé, S., Sarrazin, F., 2012. Modelling carcass disposal practices: implications for the management of an ecological service provided by vultures. J. Appl. Ecol. 49, 404–411.
- FAO, 2011. Global Food Losses and Food Waste Extent, Causes and Prevention. FAO, Rome.

Ferguson-Lees, J., Christie, D.A., 2001. Raptors of the world. Houghton Mifflin Harcourt, New York.

- Fuller, M.R., Mosher, J.A., 1987. Raptor survey techniques. In: Pendleton, B.G., Millsap, B.A., Cline, K.W., Bird, D.M. (Eds.), Raptor Management Techniques Manual. National Wildlife Federation, Washington, DC, pp. 37–65.
- Gangoso, L., Agudo, R., Anadón, J.D., de la Riva, M., Suleyman, A.S., Porter, R., Donázar, J.A., 2013. Reinventing mutualism between humans and wild fauna: insights from vultures as ecosystem services providers. Conserv. Lett. 6, 172–179.
- Gaston, K.J., Cox, D.T., Canavelli, S.B., García, D., Hughes, B., Maas, B., Martínez, D., Ogada, D., Inger, R., 2018. Population abundance and ecosystem service provision: the case of birds. Bioscience 68, 264–272.
- Graña Grilli, M., Lambertucci, S.A., Therrien, J.-F., Bildstein, K.L., 2017. Wing size but not wing shape is related to migratory behavior in a soaring bird. J. Avian Biol. 48, 669–678.
- Green, R.E., Newton, I.A.N., Shultz, S., Cunningham, A.A., Gilbert, M., Pain, D.J., Prakash, V., 2004. Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. J. Appl. Ecol. 41, 793–800.
- Hamilton, K.L., 1985. Food and energy requirements of captive barn owls *Tyto alba*. Compar. Physiol. 80, 355–358.
- Hill, J.E., DeVault, T.L., Beasley, J.C., Rhodes, O.E., Belant, J.L., 2018. Effects of vulture exclusion on carrion consumption by facultative scavengers. Ecol. Evol. 8, 2518–2526.
- Hoornweg, D., Bhada-Tata, P., 2012. What a Waste: A Global Review of Solid Waste Management. Urban development series, World Bank, Washington, DC.

Houston, D.C., 1986. Scavenging efficiency of turkey vultures in tropical forest. Condor 88, 318–323.

Houston, D.C., Cooper, J.E., 1975. The digestive tract of the whiteback griffon vulture and its role in disease transmission among wild ungulates. J. Wildl. Dis. 11, 306–313. Kirk, D.A., Currall, J.E., 1994. Habitat associations of migrant and resident vultures in

central Venezuela. J. Avian Biol. 25, 327–337. Lowney, M.S., 1999. Damage by black and turkey vultures in Virginia, 1990–1996. Wildl.

Soc. Bull. 27, 715–719.

Margalida, A., Campión, D., Donázar, J.A., 2014. Vultures vs livestock: conservation relationships in an emerging conflict between humans and wildlife. Oryx 48, 172–176.

- Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S., Dhavala, K., 2008. Counting the cost of vulture decline—an appraisal of the human health and other benefits of vultures in India. Ecol. Econ. 67, 194–204.
- Morales-Reyes, Z., Martín-López, B., Moleón, M., Mateo-Tomás, P., Botella, F., Margalida, A., Donázar, J.A., Blanco, G., Pérez, I., Sánchez-Zapata, J.A., 2017. Farmer perceptions of the ecosystem services provided by scavengers: what, who, and to whom.

Conserv. Lett. 11, e12392.

- Morales-Reyes, Z., Pérez-García, J.M., Moleón, M., Botella, F., Carrete, M., Lazcano, C., Moreno-Opo, R., Margalida, A., Donázar, J.A., Sánchez-Zapata, J.A., 2015. Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions. Sci. Rep. 5, 7811.
- Novaes, W.G., Cintra, R., 2015. Anthropogenic features influencing occurrence of Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) in an urban area in central Amazonian Brazil. Condor 117, 650–659.
- O'Bryan, C.J., Holden, M.H., Watson, J.E., 2019. The mesoscavenger release hypothesis and implications for ecosystem and human well-being. Ecol. Lett.
- Ogada, D.L., Keesing, F., Virani, M.Z., 2012a. Dropping dead: causes and consequences of vulture population declines worldwide. Ann. N. Y. Acad. Sci. 1249, 57–71.
- Ogada, D.L., Torchin, M.E., Kinnaird, M.F., Ezenwa, V.O., 2012b. Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. Conserv. Biol. 26, 453–460.
- Ortiz, N.E., Smith, G.R., 1994. Landfill sites, botulism and gulls. Epidemiol. Infect. 112, 385–391.
- Pavezi, E.F., Estades, C.F., 2016. Causes of admission to a rehabilitation center for Andean condors (*Vultur gryphus*) in Chile. J. Raptor Res. 50, 23–32.
- Platt, S.G., Gukian, T., Meraz, R.E., Ritzi, C.M., Rainwater, T.R., 2015. Exhumation of buried mammal carrion by turkey vultures. J. Raptor Res. 49, 518–520.
- Prakash, V., Galligan, T.H., Chakraborty, S.S., Dave, R., Kulkarni, M.D., Prakash, N., Shringarpure, R.N., Ranade, S.P., Green, R.E., 2017. Recent changes in populations of Critically Endangered Gyps vultures in India. Bird Conserv International:1–16.

Putman, R.J., 1983. Carrion and Dung: The Decomposition of Animal Wastes. Edward Arnold. London.

- R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Core Team, Vienna, Austria.
- Richards, N., 2011. Carbofuran and Wildlife Poisoning: Global Perspectives and Forensic Approaches. Wiley-Blackwell, Chichester, UK.

Ridgely, R.S., Gwynne, J.A., 1992. A guide to the birds of Panama: With Costa Rica, Nicaragua, and Honduras. Princeton University Press, Princeton, NJ.

- Robinson, T.P., Wint, G.W., Conchedda, G., Van Boeckel, T.P., Ercoli, V., Palamara, E., Cinardi, G., D'Aietti, L., Hay, S.I., Gilbert, M., 2014. Mapping the global distribution of livestock. PLoS ONE 9, e96084.
- Roggenbuck, M., Schnell, I.B., Blom, N., Bælum, J., Bertelsen, M.F., Sicheritz-Pontén, T., Sørensen, S.J., Gilbert, M.T.P., Graves, G.R., Hansen, L.H., 2014. The microbiome of New World vultures. Nat. Commun. 5, 5498.
- Sanchez-Zapata, J.A., Carrete, M., Gravilov, A., Sklyarenko, S., Ceballos, O., Donazar, J.A., Hiraldo, F., 2003. Land use changes and raptor conservation in steppe habitats of Eastern Kazakhstan. Biol. Conserv. 111, 71–77.
- Santangeli, A., Arkumarev, V., Rust, N., Girardello, M., 2016. Understanding, quantifying and mapping the use of poison by commercial farmers in Namibia-Implications for scavengers' conservation and ecosystem health. Biol. Conserv. 204, 205–211.
- Şekercioğlu, Ç.H., 2006. Increasing awareness of avian ecological function. Trends Ecol. Evol. 21, 464–471.
- Şekercioğlu, Ç.H., Wenny, D.G., Whelan, C.J., 2016. Why Birds Matter: Avian Ecological Function and Ecosystem Services. University of Chicago Press.
- Senzaki, M., Yamaura, Y., Shoji, Y., Kubo, T., Nakamura, F., 2017. Citizens promote the conservation of flagship species more than ecosystem services in wetland restoration. Biol. Conserv. 214, 1–5.
- Stiles, F.G., Skutch, A.F., 1989. Guide to the Birds of Costa Rica. Comstock Publishing Associates (Cornell University Press), Ithaca, NY.
- Tauler-Ametller, H., Hernández-Matías, A., Pretus, J.L., Real, J., 2017. Landfills determine the distribution of an expanding breeding population of the endangered Egyptian Vulture Neophron percnopterus. IBIS 159, 757–768.
- Torres-Mura, J.C., Lemus, M.L., Hertel, F., 2015. Plastic material in the diet of the turkey vulture (*Cathartes aura*) in the Atacama Desert, Chile. Wilson J. Ornithol. 127, 134–138.

Tryjanowski, P., Morelli, F., 2018. Effects of habitat and time of day on flock size of Turkey Vultures in Cuba (*Cathartes aura*). ZooKeys 726, 79–86.

- U.S. Environmental Protection Agency. 2012. Industrial Food Processing Waste Analyses. Available at: https://www.epa.gov/sites/production/files/2016-01/documents/ msw_task9_industrialfoodprocessingwasteanalyses_508_fnl_2.pdf.
- USDA. 2015. Cattle and Calves Death Loss in the United States Due to Predator and Nonpredator Causes, 2015. USDA–APHIS–VS–CEAH. Fort Collins, CO.
- Walters, J.R., Derrickson, S.R., Michael Fry, D., Haig, S.M., Marzluff, J.M., Wunderle Jr, J.M., 2010. Status of the California Condor (*Gymnogyps californianus*) and efforts to achieve its recovery. Auk 127, 969–1001.
- Whelan, C.J., Sekercioglu, C.H., Wenny, D.G., 2016. Bird ecosystem services: economic ornithology for the 21st century. In: Sekercioglu, C.H., Wenny, D.G., Whelan, C.J. (Eds.), Why Birds Matter: Bird Ecosystem Function and Ecosystem Services. University of Chicago Press, Chicago, IL, pp. 1–26.

Whelan, C.J., Wenny, D.G., Marquis, R.J., 2008. Ecosystem services provided by birds. Ann. N. Y. Acad. Sci. 1134, 25–60.