The avian scavenger crisis: looming extinctions, trophic cascades, and loss of critical ecosystem functions

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Abstract

Vultures, which are the only obligate vertebrate scavengers, have experienced the most rapid decline in conservation status of any group of birds over the past decade and comprise the most threatened avian functional guild in the world. Meanwhile, the vast majority of avian facultative scavenger species, such as corvids and gulls, have stable or increasing populations. We analyze the causes of this stark contrast in status and evaluate what ecological factors contribute to extinction risk for all 106 avian scavenger species. A random forest model shows that diet breadth, proportion scavenged diet, geographic realm, body mass, clutch size and taxonomy are leading predictors of extinction risk. Meanwhile, dietary toxins—most notably poisons and the veterinary drug diclofenac—are by far the most important anthropogenic threat to avian scavengers, comprising the leading cause of decline for 59% of threatened avian scavenger species and 88% of threatened vulture species. Currently, 73% of vulture species are extinction-prone (near threatened, vulnerable, endangered, critically endangered and extinct) and 77% have declining populations, while only 13% of avian facultative scavenger species

are extinction-prone and 70% have stable or increasing populations. As vultures decline, populations of many facultative scavengers are growing, causing trophic cascades from increased predation, competition, and invasion. Furthermore, vultures' highly specialized digestive systems efficiently eradicate diseases when consuming carrion, whereas facultative scavengers are more susceptible to contract and transmit diseases among themselves and to humans. We urge immediate action, particularly by regulating lethal dietary toxins, to prevent the extinction of vultures and loss of respective ecosystem services.

Highlights:

- Vultures are the most threatened group of birds, collapsing toward extinction
- 70% of avian facultative scavengers have stable or increasing populations
- Diet specialization and taxonomy are leading extinction risk predictors
- Dietary toxins are main threat for 59% of all avian scavengers, 88% of vultures
- Vulture declines expected to cause trophic cascades and disease outbreaks

Keywords: conservation ecology, avian extinction, ecosystem services, trophic cascade, functional homogenization, mesopredator release, ornithology, specialist

1 Introduction

Scavenging, or the consumption of carrion, is a common foraging strategy and a critical component of ecosystem ecology (DeVault et al., 2003). Carrion is a spatially and temporarily unpredictable food source, which birds are particularly well adapted to

exploit. Flight—particularly soaring—allows birds to cover large areas with little energetic expenditure, providing them with a competitive advantage over mammals in locating carrion. Indeed, an energetics model demonstrated that obligate vertebrate scavengers *must* be large soaring fliers (Ruxton and Houston, 2004). The 22 species of vultures in the world (the Palm Nut Vulture *Gypohierax angolensis*, is not directly related to other vultures, is not an obligate scavenger, and is excluded from this list) are the only obligate vertebrate scavengers, meaning they are near completely reliant on scavenging for food (while some vulture species, such as White-headed *Trigonoceps occipitalis* and Lappet-faced *Torgos trecheliotus* vultures, are known to kill live prey on occasion, they are highly dependent on carrion and are widely regarded as “obligate” scavengers). Vultures consume a large percentage of the carrion globally—upwards of 90% in some ecosystems (Houston, 1986).

Over the last few decades, vulture populations have declined at catastrophic rates, especially in Asia and Africa (Ogada et al., 2015; Ogada et al., 2012) and are now regarded as the single most threatened avian functional guild (obligate scavengers) in the world (Şekercioğlu et al., 2004). Meanwhile, many avian facultative scavengers (i.e. species that scavenge opportunistically)—including species of storks, gulls, ravens and crows—are among the most abundant bird species in the world, and, in many cases, have increasing population trends (IUCN, 2015). This stark contrast in the status of obligate and facultative scavengers led us to evaluate the factors causing this variable extinction risk.

In the first section of this review, we identify all avian scavengers and discuss differences in population trends between facultative, obligate and non-scavengers, and

between vulture families (*Cathartidae* and *Accipitridae*). We then analyze differences in ecological traits of all avian scavengers to determine ecological predictors of extinction risk and review the extrinsic threats to avian scavengers. We conclude by reviewing the observed and expected ecological repercussions of vulture declines.

2 Material and Methods

2.1 Scavenger classification and traits

A database containing ecological traits for all of the approximately 10,500+ bird species (hereafter “Birdbase”) was used to identify avian scavengers. Birdbase was compiled from an extensive literature survey of 248 sources initially (Şekercioğlu et al., 2004), is updated regularly with new publications (current version updated December 2015), and has been used in numerous global meta-analyses of bird populations (e.g. Şekercioğlu 2012). Eight food categories are recognized—“invertebrates”, “fruits”, “nectar”, “seeds”, “land vertebrates”, “fish”, “scavenged matter”, and “non-reproductive plant material”—and ranked as a proportion of a species’ diet (see Kissling et al. 2011). This information was used to identify a comprehensive list of species for which scavenging accounts for >10% of their diet. We set the threshold at 10% because we wanted to capture a comprehensive list of species for which scavenging is a significant and regular feeding strategy, while excluding the plethora of species that have been documented to scavenge rarely. This list of avian scavengers is a best estimate because it considers the foraging habits of every bird species in the world and is based on detailed species accounts from ornithological literature.

After identifying this group of avian scavengers, data were collected on the ecology, threat status, and population trend for each species. We also identified five families that account for 85% of all avian scavengers (Accipitridae, Laridae, Corvidae, Falconidae, and Cathartidae), and identified the threat status and population trend for each species within each family, including “non-scavengers” (species that receive <10% of their food from scavenging). The main sources for trait information, in addition to Birdbase, were the IUCN Red List of Threatened Species (2015), BirdLife International's Data Zone (2015), and the Handbook of the Birds of the World (Hoyo et al. 1992-2014). When there was inadequate or conflicting information from these sources, the primary literature was consulted. In total, 11 traits were compiled (Table 1) and incorporated into a model to determine how ecological traits predict population trends. All independent variables included have been shown to be correlated with extinction risk (i.e. diet breadth, ecological specialization, body mass, generation length, maximum eggs per clutch, migratory status, habitat, island endemism, global range size) (Davidson et al., 2009; Gaston and Blackburn, 1995; Jones et al., 2006; Murray et al., 2011; Newmark et al., 2014; Purvis et al., 2000; Şekercioğlu, 2011; Sodhi et al., 2011) and/or were of particular interest in evaluating the population trends of avian scavengers (i.e. proportion scavenged diet, social foraging). To evaluate how phylogeny is related to population trends, we included family in the model (Davidson et al., 2012).

To evaluate extrinsic threats to avian scavengers, the leading threat for each extinction-prone species (including the IUCN categories of near threatened, vulnerable, endangered, critically endangered and extinct) was identified and grouped into one of

six categories: persecution, habitat destruction, decreasing food availability, dietary toxins, fishery bycatch, or stochastic events.

2.2 Statistical analyses

Pearson's chi-square test was used to identify whether differences in threat status (threatened, non-threatened) and population trend (increasing, decreasing) between groups of scavengers were significant. Standard residual values of ≥ 2 were used to conservatively identify the direction of the relationship at the $p < 0.05$ level (Agresti, 2012). A *t*-test for independent groups was used to evaluate differences in mean values of ecological traits (i.e. global range, max clutch, average mass, etc.) between scavenger groups. All statistical tests were conducted in R, version 3.0.2 (R Core Team, 2013).

To assess the relative trend in threat status between scavengers and all other foraging guilds over the past decade, we compared the percentage of extinction-prone (near threatened, vulnerable, endangered, critically endangered and extinct) species in each of eight major foraging guilds. To classify each species, we followed the methods of Şekercioğlu et al. (2004). These guilds are defined by primary diet and include species whose diet is >50% of each of the major food categories used in the Birdbase (described above). Species that do not receive a majority of their diet from a single food category are considered omnivores. Note that the definition for scavenger in this context is different from either obligate or facultative scavenger, as used throughout the rest of the analysis. This different definition was used to replicate the classifications in Şekercioğlu et al. (2004), in order to directly compare the percentage of extinction-prone species in 2004 and 2014.

To determine the relative importance of ecological traits in predicting population trends, we used random forest (RF) analyses. RF is a powerful machine-learning technique which identifies nonlinear associations among multiple correlated predictor variables (Cutler et al., 2007), as is the case in this study. RF analyses are growing in popularity in ecological studies, particularly those evaluating extinction risk, because they have several advantages over traditional linear models, including: 1) they do not assume data independence and therefore do not require a phylogenetic control; 2) categorical and continuous variables can be simultaneously incorporated into the model without transforming data; 3) they predict outcomes based on the nested structure of variables, which allows for an accurate depiction of different pathways to the predicted outcome; and 4) they are minimally effected by outliers (Davidson et al., 2009; Jones et al., 2006; Murray et al., 2011; Newmark et al., 2014; Sullivan et al., 2006).

The accuracy of the dependent variable can be a limiting factor in this type of analysis. Accordingly, extensive efforts were made to select and verify the quality of our dependent variable. While IUCN threat status has been used in some studies evaluating extinction risk (e.g. Cardillo et al., 2005; Davidson et al., 2009; Purvis et al., 2000), we use a more simply defined population trend variable. This variable is well suited for this analysis because it avoids potential issues from non-independence of dependent and predictor variables introduced when IUCN threat status is used (i.e. range size is incorporated in IUCN threat status determination). Many of the species in this study, including vultures, raptors, corvids, albatrosses and gulls are among the most studied of bird species in the world and, accordingly, population trends were available for >96% of species in this dataset (see below). Population trends originated from BirdLife

International's Data Zone (2015), which summarizes the existing literature on each species, cites specific quantitative estimates of population trends, and weighs conflicting trend reports to decide on a final categorical trend estimate (i.e. increasing, stable, decreasing). Using the specific trend statistics included in the "Trend Justification" (BirdLife International 2015), we re-categorized our trend variable into 7 categories: rapid decline, moderate decline, slight decline, stable, slight increase, moderate increase, rapid increase (see Table 1). In this context "rapid" is indicative of >50% change in population over the past 3 generations, "moderate" of 25-50% change, and "slight" of <25% change. Species that were listed as "increasing" or "decreasing" without specific statistics were placed in the "slight" category. All species had trend data, except for four (Española Mockingbird *Mimus macdonaldi*, Andean Gull *Larus serranus*, Slaty-backed Gull *Larus schistisagus*, and Rueppell's Glossy Starling *Lamprolornis purpuroptera*), which are assumed to have stable populations. The Extinct Guadalupe Caracara *Caracara lutosa* has no trend and was excluded from the RF analysis. While extensive efforts have been made to accurately assess and categorize the population trend data for all 106 species in this analysis, some population trend determinations are based on limited research and/or expert opinions. Note that conservation actions, such as extensive efforts to restore populations of the critically endangered California Condor *Gymnogyps californianus*, influence population trends and are therefore captured in the model.

The RF analysis was run in the *randomForest* package (Liaw and Wiener, 2002) in R (R Core Team, 2013). The number of trees (*ntree*) was set to 5,000 (Newmark et al., 2014), and the optimal number of classification variables randomly sampled to calculate

the split at each node (*mtry*) was determined by the program. A large number of trees is recommended, as RF do not over-fit data (Breiman and Cutler, 2015). The predictor variables were ranked in order of importance using the “mean decrease in accuracy” (MDA) output, which measures importance by calculating the average decrease in model accuracy when each variable is excluded (Liaw and Wiener, 2002). A higher MDA is indicative of a more important variable and variables that have no importance are close to zero, or even negative (Strobl et al., 2009). While some authors have used a z-test to determine the significance of predictor variables, Strobl et al. (2009) strongly urge against this: MDA values are statistically robust in and of themselves because they are based on many bootstrapped iterations of the data fitted to the set number of regression trees (5000 in this case).

3 Results

3.1 The avian scavenger community

Scavenging is an important foraging strategy (>10% of diet) for 106 bird species from five orders and 14 families. Of these, 22 species are obligate scavengers (vultures) and 84 are facultative scavengers. Five families—*Accipitridae* (Old World vultures, eagles and hawks), *Laridae* (gulls), *Corvidae* (crows and ravens), *Falconidae* (caracaras and falcons), and *Cathartidae* (New World vultures)—account for 85% of all avian scavengers. Other species include sheathbills, petrels, shearwaters, albatrosses, storks, and starlings. Avian scavengers are truly cosmopolitan, inhabiting all continents, including Antarctica, as well as large portions of the world’s oceans. Seventy-two species are terrestrial and 34 are marine. There are 10 island-restricted species, such

as the Hood Mockingbird *Mimus macdonaldi*, which has a total range of only 70 km². Other species have immense ranges, like that of the Golden Eagle *Aquila chrysaetos*, which is found on four continents. Forty-six species are long-distance migrants, 57 are non-migrants, and 3 are partial migrants.

3.2 Threat status of avian scavengers

Of the 106 avian scavenger species, 25% (27) are extinction-prone (8 NT, 5 VU, 4 EN, 9 CR, and 1 EX), and the remaining 75% (79) are least concern (LC). Thirty-six percent (34) of species have stable populations, while 34% (41) are declining and 30% (30) are increasing (the extinct Guadalupe Caracara *C. lutosa* has no trend). Obligate scavengers have a significantly greater proportion of extinction-prone species than facultative scavengers ($\chi^2 = 34.261$, $df = 1$, $p < 0.001$), with 73% (16) of obligate scavenger species and only 13% (11) of facultative scavengers extinction-prone (Figure 1). Obligate scavengers also have a significantly greater proportion of declining species ($\chi^2 = 6.992$, $df = 1$, $p = 0.008$) than facultative scavengers, with 77% (17) of obligate scavenger species declining and only 23% (5) stable or increasing and 29% (24) of facultative scavenger species declining and 70% (59) stable or increasing (the extinct Guadalupe Caracara *C. lutosa* has no trend) (Figure 1). Average body mass is significantly greater for obligate (mean=5629 grams) than facultative scavengers (mean=1282 grams) ($t(104) = -8.79$, $p < 0.001$), generation length is significantly greater for obligate (mean=15.74 years) than facultative (mean=11.32 years) scavengers ($t(104) = -4.49$, $p < 0.001$), and clutch size is significantly greater for facultative (mean=3.75 eggs) than obligate (mean=1.50 eggs) scavengers ($t(104) = 6.96$, $p < 0.001$), illustrating that these groups have fundamentally different life histories. The *Accipitridae*

family accounts for 67% (18 of 27) of threatened species, followed by *Cathartidae*, *Diomedidae*, and *Falconidae* with two species each, and *Ciconiidae*, *Laridae*, and *Mimidae* with one species each (Figure 2).

Interestingly, within the five major families (*Accipitridae*, *Laridae*, *Corvidae*, *Falconidae*, and *Cathartidae*), facultative scavengers have a significantly smaller proportion of extinction-prone species than obligate scavengers ($\chi^2 = 30.349$, $df = 1$, $p = 0.001$) and non-scavengers ($\chi^2 = 8.518$, $df = 1$, $p = 0.003$) in their respective families. Furthermore, facultative scavengers have significantly more species with increasing population trends than obligate scavengers ($\chi^2 = 8.153$, $df = 2$, $p < 0.001$) and non-scavengers ($\chi^2 = 16.157$, $df = 2$, $p < 0.001$). This indicates that, in general, facultative scavengers are faring better than related species of obligate or non-scavengers.

3.3 Decadal change in avian guild threat statuses

Avian scavengers (in this context defined as species which receive >50% of their diet from scavenging, to directly compare with Şekercioğlu et al., (2004)) had by far the greatest increase of any foraging guild in the number of extinction-prone species over the past decade, increasing from 39% in 2004 to 56% in 2014 (Figure 3). All other foraging guilds had an increase in the percent of extinction-prone species, except for granivores (seed eaters), which had a small decrease from 20% to 19%. Carnivores (vertebrate consumers, mainly raptors) had the second largest increase, from 22% extinction-prone in 2004 to 27% in 2014.

3.4 Ecological predictors of extinction risk

In decreasing order of importance, the major predictors of declining population trend (and hence higher extinction risk) in avian scavengers are taxonomy (family), diet

breadth, proportion of diet that is scavenged, geographic realm, and body mass (Figure 4). Habitat, generation length, social foraging behavior, being island-restricted, global range size, and migratory behavior had little to no predictive power, while clutch size had intermediate predictive power.

3.5 Extrinsic threats

Dietary toxins are the most prevalent extrinsic threat to avian scavengers, cited as the primary cause of decline in 59% (16 out of 27) of all threatened or near threatened avian scavenger species, and 88% (14 out of 16) of threatened or near threatened vulture species (Figure 5). Other threats to avian scavengers include persecution (a leading driver of declines in 15% or 4 species), fishery bycatch (11%, 3 species), habitat loss (7%, 2 species), and decreasing food availability and stochastic events (4%, 1 species each) (Figure 5). Fishery bycatch is a primary threat for marine scavengers, particularly albatrosses, as they are frequently caught in long-line ocean fishing operations.

3.6 Comparisons among vulture families

Of the 22 vulture species, nine are critically endangered (CR), three are endangered (EN), four are near threatened (NT), and six are least concern (LC) (Figure 6). A significantly greater proportion of Old World vulture (OWV) species are extinction-prone than are New World vultures (NWV) ($\chi^2 = 7.091$, $df = 1$, $p = 0.007$). NWV have significantly shorter generation lengths (mean=13.73 years) than OWV (mean=16.67 years) ($t(20) = 2.38$, $p = .027$), and smaller average mass (mean=4438 grams) than OWV (mean=6185 grams), although this is not significant ($t(20) = 1.17$, $p = 0.256$). It is worth noting that all NWV are least concern (LC), except for the California Condor

Gymnogyps californianus (critically endangered (CR)) and Andean Condor *Vultur gryphus* (near threatened (NT)). Condors are the two largest vulture species, by mass, in the world, while four of the other five NWV are the smallest vultures in the world.

4 Discussion

4.1 Threat status of avian scavengers

Avian scavengers have disparate extinction risk and population trends. These differences are stark: specialist avian scavengers have declined the most precipitously of any guild over the past decade (Figure 3), and obligate scavengers are the most threatened avian functional guild in the world, with 73% of species extinction-prone (Figure 1). Meanwhile, only 13% of facultative scavengers are extinction-prone and over two-thirds (70%) of facultative scavengers have stable or increasing populations (Figure 1). Within the 5 major scavenger families (*Accipitridae*, *Laridae*, *Corvidae*, *Falconidae*, and *Cathartidae*), facultative scavengers have significantly fewer extinction-prone and declining species than obligate scavengers or non-scavengers, indicating that facultative scavengers are particularly well adapted to exploit current environmental conditions. Such sharp declines of specialist scavengers and increases in generalist species are indicative of a trend towards global functional homogenization (Clavel et al., 2011).

4.2 Ecological predictors of extinction risk

The primary predictors of extinction risk for avian scavengers are taxonomy (family), diet breadth, proportion scavenged diet, geographic realm, body mass, and clutch size (Figure 4). These results support and augment existing models of extinction risk. It was

298 expected that family would be the leading predictor of extinction risk, because
299 Accipitridae vultures represent the majority of threatened species. Nonetheless other
300 metrics had strong predictive power, indicating that there are broader ecological
301 conclusions to be drawn from the model. Diet breadth and proportion scavenged diet, in
302 particular, were leading predictors of extinction risk in avian scavengers. Diet
303 specialization is a known predictor of extinction risk in a wide range of taxa, including
304 plants (Rooney et al., 2007), fish (Munday, 2004), mammals (Fisher et al., 2003), and
305 birds (Şekercioğlu 2011, 2012), and population declines of birds have been shown to be
306 strongly related to diet preference (Şekercioğlu et al., 2004). Geographic realm was
307 another powerful predictor in our model, indicating that different species distributions,
308 species-specific traits and, perhaps, anthropogenic practices on different continents
309 play a role in scavenger declines. For example, the disparate use of poisons and
310 veterinary drugs and differing human attitudes and degrees of governmental protection
311 for wildlife are likely among the most important factors driving variations in extinction
312 risk among avian scavengers, and the geographic realm variable may be capturing
313 some of this influence. Body mass is another important predictor in our model, and has
314 been shown to be an important factor in population declines in numerous studies across
315 a wide range of taxa (Davidson et al., 2012; Dulvy and Reynolds, 2002; Gaston and
316 Blackburn, 1995; Purvis et al., 2000). Large body size correlates with many other
317 ecological traits that factor in extinction risk, including delayed maturation, slow
318 reproductive rate, low population densities, and large individual home ranges (Purvis et
319 al., 2000). Many avian scavengers, including vultures, raptors, albatrosses, and storks,
320 are among the largest birds in the world. Finally, clutch size, like body mass, is another

proxy for life history strategy, with smaller clutches indicative of *K*-selected species that are highly susceptible to increased adult mortality. Somewhat surprisingly, generation length (another proxy for overall life history), global range size, social foraging behavior, migratory status, being island-restricted, and habitat (broadly, terrestrial or marine) had no meaningful predictive power in the model. This is likely due to correlation with other variables in the analysis that are better predictors.

4.3 Extrinsic threats

The primary extrinsic threat for extinction-prone avian scavenger species is dietary toxins, followed distantly by persecution, fishery bycatch (a major factor in marine scavenger declines), habitat destruction, decreasing food availability, and stochastic events (for the range-restricted island-endemic Española Mockingbird *Mimus macdonaldi*). Dietary toxins disproportionately threaten vultures, being the primary cause of decline for 86% (14 of 16) of threatened vulture species (Figure 5). The most extreme example of dietary toxins causing declines comes from South Asia, where vulture populations declined by as much as 99.9% from 1992-2007 (Prakash et al., 2007). Poisoning from the anti-inflammatory veterinary drug diclofenac caused catastrophic declines of Oriental White-backed *Gyps bengalensis*, Long-billed *Gyps indicus*, Slender-billed *Gyps tenuirostris*, Egyptian *Neophron percnopterus*, and Red-headed *Sarcogyps calvus* vultures in India, Pakistan, and Nepal (Green et al., 2004). Vultures were exposed to diclofenac when they consumed carcasses of livestock that died within a few days of drug treatment (Oaks et al., 2004). Due to its extreme lethality to vultures, which manifests as kidney failure, and vultures' highly social foraging habits,

only <0.8% of livestock carcasses would have needed to contain diclofenac to cause such declines (Green et al., 2004).

Dietary toxins are causing vulture populations in Africa to crash, as well (Ogada et al., 2015; Ogada et al., 2012). The deliberate poisoning of mammalian carnivores, such as jackals, hyenas and lions, to avenge the loss of livestock is common in Africa and has led to widespread unintentional poisoning of vultures (Ogada et al., 2012). With the recent escalation of rhino and elephant poaching across the continent, poachers are also now intentionally poisoning vultures, whose circling over carcasses can quickly lead authorities to the crime site (Ogada et al., 2015). *Carbofuran*, a widespread and cheap insecticide that is highly toxic is a primary culprit for such poisonings (Otieno et al., 2010; Virani et al., 2011). However, numerous types of poisons have been used throughout Africa, including *Strychnine* and synthetic organic pesticides. These poisons are incredibly effective at killing wildlife. For example, in 2013, a single poisoned elephant carcass in Namibia killed as many as 600 vultures (Smith, 2014). As a result of such poisoning, as well as other mortality factors, the Bearded Vulture *Gypaetus barbatus* has declined by 70%, while seven other species have declined by 80% or more over three generations across Africa (Ogada et al., 2015). Accordingly, the IUCN (2015) uplisted four vulture species (Hooded *Necrosyrtes monachus*, Ruppell's *Gyps rueppellii*, White-backed *Gyps africanus*, and White-headed *Trigonoceps occipitalis*) to critically endangered (CR) in 2015, while another three species (Egyptian *Neophron percnopterus*), Lappet-faced *Torgos tracheliotus*, and Cape *Gyps coprotheres*) are listed as endangered (EN), and the Bearded Vulture *G. barbatus* is considered near threatened (NT). In other regions of the world, including Europe and the Americas,

dietary toxins, including rodenticides, insecticides (i.e. DDT), and lead from spent ammunition are contributing to mortalities of avian scavenger species. Thus, scavengers' vulnerability to toxins makes them harbingers of environmental pollutants in the food chain, which surely impact countless species across trophic levels.

4.4 Comparisons among vulture families

There are 22 species of vultures in the world in two distinct lineages: the New World vultures (NWV) in the *Cathartidae* family, and Old World vultures (OWV) in the *Accipitridae* family. NWV and OWV share many similar adaptations for scavenging, including large, broad wings adapted for long-distance, efficient soaring flight, and featherless heads, an adaptation for thermoregulation and/or to minimize contamination while feeding on carcasses (Ward et al., 2008). Vultures in both families are K-selected species: they are long-lived, large-bodied and have slow reproductive rates. Interestingly however, NWV are significantly less threatened with extinction. Differing human practices and governmental policies for the protection of wildlife may factor in the disparate extinction risk of these similar groups of birds on different continents. Our results also indicate that ecological traits may also play a role.

NWV have, on average, shorter mean generation lengths and smaller body masses than OWV, indicating a faster overall life-history strategy, which makes them somewhat less vulnerable to increased adult mortality. In support of this argument, the largest and slowest-reproducing NWV, the California *G. californianus* and Andean *V. gryphus* condors, are the only threatened NWV (critically endangered (CR) and near threatened (NT), respectively). We recognize that these factors are not necessarily the drivers of differences in these families, but find it noteworthy that important predictors of extinction

risk in the overall dataset are significantly differentiated among these families. Perhaps a more important driver of the differences in threat status between vulture families, however, is differences in foraging ecology between the families. In a key innovation that differentiates NWV from OWV, NWV in the genus *Cathartes* have a highly developed sense of smell, which allows them to locate carcasses deep in forest, even when completely buried (Houston, 1985). They then lead other NWV species to carcasses that they would otherwise be unable to find. OWV, contrastingly, depend on vision to locate carcasses. NWV thus often eat smaller carcasses, including monkeys, sloths, birds and rodents, while OWV primarily eat larger carcasses, predominantly large ungulates. Trophic dynamics dictate that smaller animals are more numerous and ubiquitous in the environment, making them a more spatially and temporarily reliable food source. We also suspect that larger carcasses are more likely to contain environmental toxins, whether from veterinary drugs, intentionally applied poisons, or bioaccumulation. Furthermore, because of the social foraging habits of scavengers, a large carcass containing dietary toxins can be fed on by dozens (or even hundreds) of scavengers, whereas only a few individuals can feed on a small carcass. We suggest that this makes OWV at least somewhat more susceptible to poisoning than NWV—particularly those species in the *Cathartes* genus, which include no threatened species. While forest-dwelling NWV may be more susceptible to habitat loss (deforestation) than OWV, the main drivers of acute mortality—namely dietary toxins—are likely largely responsible for the apparently differentiated rates of decline between vulture families.

4.5 Repercussions of vulture declines

While research documenting vulture declines is extensive (Manga, 2006), there is little research investigating consequences of these declines (Ogada et al., 2012). When vulture populations are reduced or removed from an ecosystem, carrion becomes increasingly available to other organisms, including facultative scavengers, insects, and microorganisms, in a form of terrestrial eutrophication. Furthermore, carcasses can serve as a breeding ground and vector for many diseases that impact wildlife, livestock, and humans.

There is strong competition among vertebrates, invertebrates, and microbes to use carrion (Putman, 1983). Nonetheless, vertebrate scavengers consume an estimated 75% of the available carrion globally (DeVault et al., 2003; Richardson, 1980). Vultures play a major role in locating and recycling carrion. In Central and South America, 60-95% of carcasses are located and consumed by vultures (Houston 1985, 1994). In these studies, most carcasses were located within 12 hours by Turkey Vultures *Cathartes aura*, whereas mammals rarely located carcasses. Due to their competitive advantage in finding and consuming carrion, Houston (1994) suggests that vultures likely consume more meat in Central and South America than all mammalian predators combined. Similarly, before their recent decline, vultures in the Serengeti of East Africa were estimated to consume about the same amount of meat (370 kg/km²/year) as all mammalian carnivores in the ecosystem (Houston, 1983). Thus, rapid declines in vulture populations are expected to have profound and largely unanticipated impacts on ecosystem ecology.

First of all, mesopredator release is a major concern when apex predators are lost from an ecosystem (i.e. Soule et al., 1988), and we propose that this phenomenon can

434 take place following vulture declines. There is growing evidence that trophic cascades
435 follow the collapse of vulture populations. Due to facultative scavengers' faster
436 reproductive rates (which we demonstrate here, i.e. shorter generation lengths and
437 larger clutch size), they can reproduce more quickly when there are abundant
438 resources. Over two-thirds (70%) of all avian facultative scavenger populations are
439 currently stable or increasing, and they are faring better than obligate or non-
440 scavengers within their respective families. Most facultative scavengers are also
441 predators, and they can cause drastic top-down effects via predation, invasion, and
442 competition when their numbers increase. Examples of subsidized avian facultative
443 scavenger populations impacting lower trophic levels abound. For example, the
444 California Gull *Larus californicus* population in the San Francisco Bay increased from
445 <1,000 breeding pairs in 1982 to >33,000 in 2006, as a result of increased human
446 refuse (Ackerman et al., 2006). This subsidized population was responsible for the
447 depredation of 61% of American Avocet *Recurvirostra americana* chicks and 23% of
448 Black-necked Stilt *Himantopus mexicanus* chicks at a shorebird colony (Ackerman et
449 al., 2006). Nest predation increased in Ohio with the presence of facultative scavengers
450 along a rural to urban gradient (Rodewald et al., 2011). In the Canary Islands, predation
451 risk for ground nesting birds was higher near "vulture restaurants", due to the
452 subsidization of facultative scavenger populations at these sites, which, in turn, preyed
453 on ground-nesting birds (Cortés-Avizanda et al., 2009). Large gull populations even
454 increase whale mortality by feeding on their blubber when whales surface to breathe
455 (Marón et al., 2015).

Facultative scavengers are also often very successful invasive species: of the 56 animals on the 100 Worst Invasive Species list, 27—or nearly half—are facultative scavengers (Lowe et al., 2000; Wilson and Wolkovich, 2011). In a particularly notorious example, the facultative scavenging habits of rats have, at least in part, enabled them to invade ecosystems. Ship Rats *Rattus rattus* are associated with global declines or extinctions of 60 vertebrate species (Towns et al., 2006). We expect the increased availability of carrion caused by vulture declines to exacerbate the magnitude and variety of such impacts, allowing some populations of facultative scavengers, mesopredators, and invasive species to increase in areas where vultures have declined, from human-dominated to remote, largely untrammelled ecosystems. Climate change may further exacerbate this trend, as generalist, highly adaptable facultative scavengers are expected to be at a competitive advantage, as species ranges shift and trophic dynamics are strained (Wormworth and Sekercioğlu, 2011).

Vultures also provide an important ecosystem service by quickly consuming carcasses that would otherwise fester with disease (Markandya et al., 2008; Şekercioğlu et al., 2004). Carcasses provide a reservoir and vector for many disease agents, including Ebola, plague, anthrax, rabies, etc. (e.g. Monroe et al., 2015; Ramsden and Johnston, 1975). Vultures have highly acidic stomachs (with a pH as low as 1) which kill most viruses and bacteria that are ingested (Houston and Cooper, 1975). In Kenya, the absence of vultures at carcasses correlated with longer decomposition times, increased numbers of mammals at carcasses (primarily hyenas and jackals), and increased direct contact between mammals at carcasses (Ogada et al., 2012). Increased contact among facultative scavengers is expected to increase the

potential for disease transmission between themselves and ultimately to humans. South Asia provides an alarming example of this. In India, vulture populations declined by approximately 99% between 1992 and 2003 (Markandya et al., 2008). During this same time period, feral dog numbers increased by 7 million, despite widespread sterilization programs (Markandya et al., 2008). This increase in dogs resulted in 39 million dog bites from 1992 to 2003, causing an estimated 48,000 human rabies mortalities in India (Markandya et al., 2008).

When sufficient scavenger populations are absent, alternative methods to dispose of animal carcasses can be highly controversial, ineffective, and/or expensive. For example, in the outbreak of foot and mouth disease (FMD) in the United Kingdom in 2001, over 6.5 million animals were disposed of and/or slaughtered (Scudamore et al., 2002). Carcasses were initially buried on farms, but this was soon banned, due to concerns about infecting water supplies. Incineration of carcasses drew widespread public opposition due to concerns for the smell and health risks of smoke. Eventually, the UK government resorted to mass burials in engineered landfills. The Netherlands was also hard hit by the FMD outbreak and, to manage the issue, they slaughtered infected livestock and froze them en-masse due to a lack of adequate disposal options (de Klerk, 2002). The vulture population crash in South Asia even led to a religious crisis among Parsis, a sect of Zoroastrians, which relied on vultures to consume the body of their deceased in “sky burials” for millennia. With skies devoid of vultures, Parsis have struggled to find a method to dispose of their dead that is harmonious with their religious beliefs. These examples foreshadow potential problems resulting from functional extinctions of vultures.

5 Conclusions

In recent decades, growing concern for the plight of vultures has led to increasing research and conservation on this critical functional group (Manga, 2006), achieving important results. Examples include successful efforts to save the California Condor *G. californianus* from the brink of extinction and to restore populations across western North America (Walters et al., 2010), widespread reintroductions of the Bearded Vulture *G. barbatus* in Europe (Frey and Walter, 1989; Simon et al., 2007), and the rapid response of India, Pakistan, and Nepal to ban the use of diclofenac for veterinary purposes, which led to the stabilization of crashing vulture populations there (Cuthbert et al., 2011; Prakash et al., 2012). While this trend is encouraging, more research and conservation actions are urgently needed, particularly in Africa (to stem rapid declines), South Asia (to restore critically endangered populations) and South and Central America (to investigate the status and trends of little studied species, particularly the Andean Condor *V. gryphus*, and King *Sarcoramphus papa*, Greater Yellow-headed *Cathartes melambrotus*, and Lesser Yellow-headed *Cathartes burrovianus* vultures). Furthermore, there is a pressing need for more research valuating the ecosystem services provided by vultures and investigating the potential ramifications for their declines (e.g. Markandya et al., 2008; Ogada et al., 2012). In particular, we urge research: 1) quantifying how much carrion vultures consume, 2) investigating the role of vultures in eradicating and/or disseminating disease, and 3) determining how and to what degree vultures regulate populations of facultative scavengers and pestilent insects.

While further research is needed to better understand the consequences of vulture declines, it is clear that the widespread availability and application of dietary toxins is the most acute threat to their populations, as well as many other scavenging species. In order to prevent imminent extinctions of vultures and loss of invaluable and largely underappreciated ecosystem services, we urge regulations at local, regional, and global scales in order to inhibit the production, import, dissemination and/or misuse of lethal dietary toxins. While vultures have an intrinsic biological susceptibility to extinction in the modern world, the causes for their declines are definitively anthropogenic.

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728

729 **Table 1.** Description of traits used in the random forest (RF) analysis.

Trait	Description/source
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<i>Population trend (i.e. Extinction risk)</i>	From BirdLife's "Trend Justification" (BirdLife International 2015). Categorized as: rapid decline (-3), moderate decline (-2), slight decline (-1), stable (0), slight increase (1), moderate increase (2), rapid increase (3). "Rapid" is indicative of >50% change in population over the past 3 generations, "moderate" of 25-50% change, and "slight" of <25% change. Species that were listed to be experiencing population increases or decreases without specific statistics were placed in the "slight" category. All species in this study had trend data, except for four (Española Mockingbird, Andean Gull, Slaty-backed Gull, Rueppell's Glossy Starling), which are assumed to have stable populations. The Extinct Guadalupe Caracara has no trend and was excluded from the random forest analysis.
<i>Proportion scavenged diet</i>	The proportion (from 0 to 1) of a species' diet from scavenging on carrion. This variable originated from Birdbase, and was augmented by the Handbook of the Birds of the World (Hoyo et al., 1992) and primary literature on species (Feare and Craig, 1999; Ferguson-Lees, 2001; Howell and Dunn, 2007; Madge and Burn, 2001; Olsen and Larsson, 2013, 2004).
<i>Diet breadth</i>	The number of major food categories (from insects, fruits, nectar, seeds, vertebrates, fish, scavenged matter, non-reproductive plant matter) each bird uses. Ranked from 1 (the most specialized foragers, using only 1 major food type) to 8 (the most generalist foragers, using all 8 major food types).
<i>Body mass</i>	Body mass, in grams, from Birdbase.
<i>Generation length</i>	The average age of breeding adults in the population (BirdLife International 2015).
<i>Max clutch</i>	The maximum number of eggs laid in a clutch (Birdbase)
<i>Migratory status</i>	Non-migrant, partial migrant, or full migrant (Birdbase).
<i>Habitat</i>	Either terrestrial or marine.
<i>Island restricted</i>	Island-restricted or not. Wide-ranging species of seabirds that breed on islands were defined as island-restricted because they are vulnerable to island-related threats. These species are Hall's giant-petrel <i>Macronectes halli</i> , Antarctic giant-petrel <i>Macronectes giganteus</i> , great shearwater <i>Puffinus gravis</i> , white-capped albatross <i>Thalassarche steadi</i> and Campbell albatross <i>Thalassarche impavida</i> .
<i>Global range</i>	Global range, in km ² (Birdlife International 2015).
<i>Social foraging</i>	A rank of how socially a species forages: 1 = alone, 2 = in pairs, 3 = in small to medium sized groups, 4 = in a highly social manner with mixed species flocks.

Realm

Species were classified into 10 groups based on their geographic range: Australia (AU) (including New Zealand), East Asia (EA) (including India, the Indo-Malayan tropics, and southeast Asia), Afrotropical (AF) (continental Africa), Neotropical (NT) (southern Mexico through South America), Nearctic (NE) (central Mexico through North America), Palearctic (PA) (Europe and Asia minus EA above), Oceanic (OC) (oceans and oceanic islands), Old World (OW) (range extends over more than one of AU, EA, AF, PA), New World (NW) (range extends over NE and NT), or Cosmopolitan (CO) (range extends over NW and OW).

730

731

732 **Figure 1.** The percent of obligate and facultative scavenger species that are extinction-
 733 prone and that have declining and stable or increasing populations. “Extinction-prone”
 734 species include those in the IUCN Red List category of Near Threatened, Vulnerable,
 735 Endangered, Critically Endangered, or Extinct (IUCN, 2015).

736

737 **Figure 2.** IUCN Red List status for all avian scavengers by family. Least Concern = LC,
 738 Near Threatened = NT, Vulnerable = VU, Endangered = EN, Critically Endangered =
 739 CR, Extinct = EX (there were no EW or DD species in this dataset)(IUCN, 2015).

Figure 3. The percent of species in each of 9 major feeding guilds that are extinction-prone (NT, VU, EN, CR, EX) in 2004 and, a decade later, in 2014 (IUCN, 2014). Note the particularly sharp increase in the threat status of avian scavengers.

Figure 4. Permutation importance scores for a random forest model evaluating the importance of ecological traits in predicting extinction risk in avian scavengers. Predictor variables are ranked in order of importance using the “Mean Decrease in Accuracy” (MDA) output, which measures the importance of each variable by calculating the average decrease in the model’s accuracy when that variable is excluded from the model. A higher MDA is indicative of a more important variable. See Table 1 for a full description of the variables.

Figure 5. Summary of the top extrinsic threats for each extinction-prone (Near Threatened, Vulnerable, Endangered, Critically Endangered, and Extinct) avian scavenger species. Threats are from species accounts in the IUCN Red List (IUCN 2015). Each threat was grouped into one of six main categories: dietary toxins, persecution, fishery bycatch, habitat destruction, decreasing food availability, or stochastic events.

760

761 **Figure 6.** IUCN threat status for all vulture species, by family (IUCN 2015). *Accipitridae*
 762 vultures are significantly more extinction-prone than *Cathartidae* vultures.