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Review

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. Of the 22 vulture species, nine are critically endangered, three are endangered, four are near threatened, and six are least concern. 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.

Contents

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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 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 (Buechley and Şekercioğlu, 2016; Ogada et al., 2012a, 2012b, 2015) and are now 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