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The corrupted carnivore: how humans are rearranging the return of the carnivore-scavenger relationship

After centuries of declining abundance and distribution (Ripple et al. 2014), apex carnivores are repatriating parts of their historical range across Europe (Chapron et al. 2014), North America (Gompper et al. 2015), South America (Novaro and Walker 2005), and Asia (Athreya et al. 2013). These recoveries are not occurring only in remote wildlands, but are increasingly found in landscapes featuring a strong human presence (Kuijper et al. 2016). With their return to these landscapes, there is hope that many of the services carnivores provide will return too (Ripple et al. 2014). Indeed, even at low densities, carnivores can regulate prey populations, induce trophic cascades that release plants from herbivory, control mesopredators, reduce and confine disease outbreaks, improve human health, control exotic species, enhance carbon storage and support a more diverse community of organisms (Estes et al. 2011). These are lofty expectations for this guild, some of which will be realized. Given that in many instances carnivore recolonization will be to strongly modified and even entirely novel landscapes, it is likely that the functional role of carnivores will be importantly altered (Kuijper et al. 2016), only partially realized (Moss et al. 2016), or in some cases, completely different. Nowhere will this altered role of carnivores be more evident than in their relationship with obligate scavengers.

Scavenging, the consumption of carrion, is widespread among diverse taxa, represents a unique and substantial form of energy transfer between trophic levels and is central to nutrient cycling, disease dynamics, and the structuring of ecological communities (Wilson and Wolkovich 2011). Apex predators provide access to essential food resources for many species of scavengers and by leading scavengers to kills, and stripping the hide of prey, reduce both the search and handling time for scavengers. Thus, predator kills are often preferred over non-preyed carcasses (Moleón et al. 2014). Prehistorically, humans were scavengers and exploited carnivore kills, but as societies became increasingly pastoral, carnivore kills were no longer needed and carnivores were viewed as strict competitors. Consequent eradication efforts, including poisoning, greatly reduced carnivore populations globally (Ripple et al. 2014).

Now, we are witnessing a moment where rebounding carnivore populations and increased poisoning are colliding once again. Obviously, this will have implications for carnivores but also for the ecological interactions that they are part of, especially for facultative and obligate scavengers that utilize the carrion that carnivores leave behind. For no guild is this more apparent than among vultures – obligate avian scavengers – nature's most successful vertebrate scavenger but one of the most threatened guilds globally (Ogada et al. 2012). Because of their strict dependence on ephemeral carrion resources, vultures are highly sensitive to toxins present in carrion, such as lead pellets in hunted game, residual pharmaceutical compounds in livestock remains, and intentionally poisoned carcasses (Ogada et al. 2012). Given their behavioral strategies – notably aggregating in large numbers at carcasses – they are disproportionately vulnerable to catastrophic die-offs in a single poisoning event.

In the arid lands of South America, carnivores and scavengers interact strongly and represent an illustrative case study (Fig. 1). Here, Andean condors (*Vultur gryphus*) scavenge wild camelid carcasses (*Lama guanicoe* and *Vicugna vicugna*) killed by pumas (*Puma concolor;* Perrig et al. 2017, Donadio et al. 2012). In areas undisturbed by humans, puma predation accounts for >90% of camelid carcasses (Donadio et al. 2012). Andean condors rely almost exclusively on camelid carcasses – all condors observed were feeding within utilized camelid carcasses, 85% of which resulted from puma predation, and the majority (88%) of condor diet is camelids (Perrig et al. 2017). This tri-trophic relationship was likely widespread prior to the establishment of ranching, especially before large-scale sheep operations that ultimately covered vast regions of South America. The near complete removal of pumas and camelids was associated with ranching in some areas (Novaro and Walker 2005). Predators were commonly removed by poisoning carcasses of both domestic and wild herbivores. Given the strong link of predator-killed carcasses with Andean condors, they too were poisoned. Beginning in the 1980s, many ranches were abandoned because of economic factors and range degradation. This abrupt change in land management created an opening for native wildlife to recolonize, including pumas and their herbivore prey (Novaro and Walker 2005), presumably with potential benefits to Andean condors.

However, livestock ranching steadily recovered along with the rebounding pumas, resulting in a new and slightly different predator-ranching conflict. Currently, the historic puma-camelid predator-prey relationship has been diminished and, at least partially, supplanted with a puma-livestock one (Fig. 1). Consequently, condors have come to rely heavily on livestock carrion (nearly 60% of their diet) in human-dominated landscapes (Lambertucci et al. 2009). Ranchers looking to reduce livestock depredation poison carrion of both livestock and camelids, killing many condors (Fig. 1). Indeed, in January 2018, 34 Andean condors died from poisoning, representing the single largest mortality event documented within the recent decades (Fig. 1). A simple search (Google, January 2018, key words: "envenenamiento" AND "condor Andino" ["poisoning" and "Andean condor"]) of press releases revealed that since 2006 at least 18 poisoning events were documented in Argentina

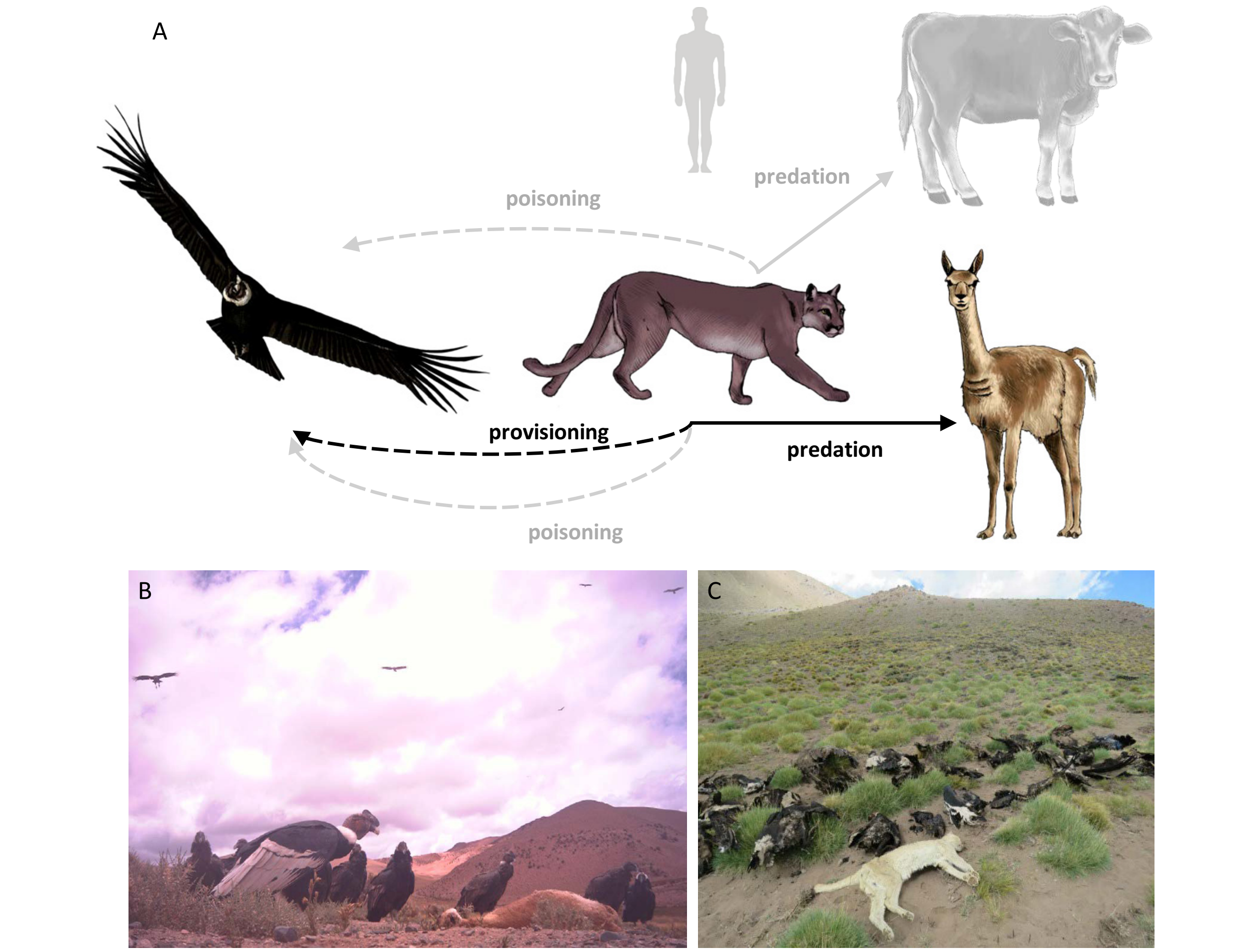

FIG. 1. (A) Historically, apex carnivores (e.g., pumas), killed and consumed large herbivores (e.g., South American camelids) with leftover carrion being provisioned to scavengers (e.g., Andean condors). With pastoralism, came the arrival of livestock, which carnivores depredated and came into conflict with humans who poisoned carrion of both domesticated and wild herbivores. This poisoning altered the fundamental relationship of carnivores with scavengers, flipping this relationship from one of provisioning to poisoning (solid and dotted lines denote a direct and indirect interaction, respectively; black lines = historic, grey = anthropogenic); (B) Andean condors in a protected area of Argentina, consuming a puma-killed vicuna; (C) A puma and 34 condors that were intentionally poisoned with the carbamate pesticide, carbofuan, during a single event in Mendoza province, Argentina on January 2018 (Photo: Courtesy of Prensa Secretaría de Ambiente Mendoza).

alone, resulting in the poisoning of at least 71 individuals. Poisoning has been reported in almost every other country of South America that condors inhabit. Some poisoning events are large in scale (e.g., in Chile with 22 poisoned birds at one carcass; Pavez and Estades 2016), while other smaller poisoning events are occurring in countries like Colombia or Ecuador where the species is critically endangered. Moreover, poisoning vultures is not exclusive to South America: large vulture die-offs have been reported in Europe, Asia and Africa (Ogada et al. 2012).

Humans affect ecological interactions directly and indirectly by reducing or removing one or more species, sometimes with cascading effects (Ripple et al. 2014). Here, we hypothesize that the recent recolonization of native predators and their ungulate prey will reestablish an important predator-prey interaction, but with unintended and unexpected consequences. In particular, we predict that as predator control keeps pace with rebounding carnivore populations, increased conflict will lead to increased poisoning of carrion sties. While poisoning will certainly impact carnivores, we predict that the effects will be most apparent among scavengers, particularly obligate avian scavengers. Essentially, then, humans will rearrange the carnivore along at least one functional axis, flipping the scavenger-carnivore relationship upside-down from positive (i.e., provisioning) to a negative (i.e., poisoning) one. Future research should evaluate this relationship between carnivore recovery and the frequency of poisoning events, identify the species of carnivores and scavengers involved, and explore the demographic consequences of predator-provisioning versus -poisoning, and predict the social-environmental scenario in which predator-scavenger relationship is most vulnerable. Ultimately, ecologists need to recognize that the return of species, especially carnivores, might result in ecological interactions that are exactly the opposite of our expectations, and work to avoid those unwanted outcomes.

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