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The Vulture in the Sky and the Hominin on the Land: Three Million Years of Human–Vulture Interaction

Federico Morelli[*], Anna Maria Kubicka[†], Piotr Tryjanowski[‡] and Emma Nelson[§]

[*]*University of Zielona Góra, Faculty of Biological Sciences, Institute of Biotechnology and Environment Protection, Zielona Góra, Poland; and Czech University of Life Sciences Prague, Faculty of Environmental Sciences, Department of Applied Geoinformatics and Spatial Planning, Prague, Czech Republic*

[†]*Adam Mickiewicz University in Poznan , Faculty of Biology, Department of Human Evolutionary Biology, Poznan, Poland*

[‡]*Poznan University of Life Sciences, Institute of Zoology, Poznan, Poland*

[§]*School of Medicine, University of Liverpool, Liverpool, UK; and Archeology, Classics and Egyptology, University of Liverpool, Liverpool, UK*

Address for correspondence: Anna Maria Kubicka, Umultowska 89, Poznan 61-614, Poland. E-mail: akubicka@amu.edu.pl

ABSTRACT Vultures and humans have been sympatric for millions of years and evidence from the archaeological and historical records suggests interdependence over long periods. Like other species, early hominins probably used these birds to locate carcasses in the landscape. With the evolution of large-bodied and more encephalized hominins, the quest for high-quality food would have intensified. Vultures used as beacons for meat may have been particularly important to hominins dispersing out of Africa, facilitating the occupation of new landscapes. Neanderthals and prehistoric modern humans incorporated vulture parts into their culture, and while the symbolic and ritualistic significance of the birds may have varied through time and across cultures, their link with positive life forces is apparent. More recently, the intensification of farming and modern sanitary restrictions, as well as the spread of human populations, has led to the radical decline in vulture populations throughout the world. Without commitments by governments to fund vulture conservation programs, the ability to preserve many species may be limited over the long term. In this review paper we discuss the ability of vultures to act as beacons signaling meat in the landscape and our changing relationships with these enigmatic birds through a shared history. Within this narrative, we outline why vultures are fundamental to maintaining our ecosystem and should therefore be protected.

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Vultures and hominins probably began to interact in the Late Pliocene when early hominins started to incorporate meat into their diet (Moleón et al. 2014). As hominins and vultures occupied the same habitats and scavenged the same medium/large mammals, they likely competed for access to carcasses alongside other scavengers (Blumenschine 1987; Robert and Vigne 2002; Domínguez-Rodrigo and Pickering 2003; Marín-Arroyo and Margalida 2012; Margalida and Marín-Arroyo 2013). Just as modern humans and terrestrial scavengers, such as hyena (family Hyaenidae), lion (*Panthera leo*) and African wild dog (*Lycaon pictus*), use vultures as a means of locating carcasses in today's landscapes (O'Connell, Hawkes and Blurton 1988; Ruxton and Wilkinson 2012), extinct hominins probably also used these birds as beacons to find food.

Vultures, like humans, have slow reproductive rates, long lives, and eat meat (Cordain et al. 2000; Ogada, Keesing and Virani 2012). However, unlike humans, vultures occupy almost exclusively a scavenging niche (Ogada et al. 2012). These birds of prey are such efficient scavengers that in some areas of Africa their strategies allow them to consume more meat than all other carnivores combined (Ogada, Keesing and Virani 2012). Aerial searching enables vultures to locate kill sites over a wide region, including dense tropical rainforests (Houston 1986; van Dooren 2011), thus providing them with a major advantage over other scavengers. The birds can remain in the air for long periods of the day by exploiting energy-saving thermals and, while aloft, they observe each other's behavior enabling them to extend their foraging range even further (Newton 1979; Ogada, Keesing and Virani 2012). The largest old-world vultures, griffon vultures (*Gyps fulvus*), may even take advantage of seasonal changes across continents, scavenging on natural deaths of herbivores at the end of the dry season in Africa and Asia, and in the late winter in Europe (Houston 1983).

The presence of vultures and other scavenging birds, therefore, would have been an effective indicator of foraging zones for observant hominins. Vultures and migrating ungulate herds may even have been instrumental in facilitating early hominin dispersal out of Africa (Antón et al. 2002). In turn, humans, via animal domestication and continual range expansion, have provided vultures with opportunities to extend their scavenging territories (e.g., Agudo et al. 2010). Over millions of years human and vulture evolution have been intertwined. Thus, our relationships with vultures could be considered one of the most ancient interspecific relationships of the genus *Homo*.

Interactions between Early Hominins and Vultures

Long, early phases of human prehistory focused on adaptation to different environmental conditions, particularly the search for adequate food supplies (Blumenschine 1987; Lee 2005). At 3.39 Mya there is putative evidence of cut marks on fossilized bones from Dikika, Ethiopia, suggesting that *Australopithecus afarensis* may have been the first hominin to scavenge and butcher carcasses, although this may have happened only rarely (McPherron et al. 2010). Significantly, this evidence falls close to a turnover in the carnivore guild (3.5 Mya; Turner and Anton 1998; Werdelin and Lewis 2013).

Around 2.5 Mya there is further change in the carnivore guild and the appearance (2.4 Mya) of the genus *Homo* (*Homo habilis sensu lato*) (Turner and Anton 1998; Robson and Wood 2008; Werdelin and Lewis 2013). Cranial and dental changes with the evolution of the genus suggest a shift in diet (Organ et al. 2011; Ungar 2012). In the archaeological record, there is incontrovertible evidence of stone-tool use and cut marks on fossilized bones alongside a gradual increase in dietary breadth, which includes animal tissues (Semaw et al. 1997; de Heinzelin et al. 1999; Antón, Potts and Aiello 2014). The incorporation of meat in the diet appears to have been a critical adaptation that facilitated this phase of human evolution (Bunn and Ezzo 1993; Larsen 2003; Navarrete, van Schaik and Isler 2011; Ungar 2012). The regular use of stone tools would have enabled hominins to acquire meat more efficiently than their evolutionary ancestors, and using signals from animals to detect carcasses in the landscape (see Danchin et al. 2004; Valone 2007) may have quickly become part of the hominin behavioral repertoire.

At around 1.9 *Mya Homo erectus* appears in the fossil record. This species is associated with profound changes in body and brain size, as well as life history (Wood and Collard 1999; Shultz, Nelson and Dunbar 2012). The marked increase in brain size in *H. erectus* (40% larger than *H. habilis*, and 80% larger than *A. afarensis*; Shultz and Maslin 2013) is indicative of a shift in social organization (Aiello and Dunbar 1993; Aiello and Kay 2002; Isler and van Schaik 2012). The high metabolic demands of a large brain and body, as well as an increase in social group size, would have increased the pressure to secure a stable supply of protein and fat laden food necessary to support these changes (Navarrete, van Schaik and Isler 2011).

At this time, relationships with vultures likely intensified. Vulture signals could have become more securely incorporated into a suite of adaptive strategies, which helped buffer hominins against the environmental uncertainty (e.g., Wrangham et al. 1999; Layland and Brown 2006). Larger body size is associated with larger home-range size in mammals, with carnivores having the biggest ranges (Shipman and Walker 1989; Antón, Leonard and Robertson 2002). Thus, larger body size and the inclusion of meat in the diet is consistent with *H. erectus* ranging further (Antón, Leonard and Robertson 2002; Grove, Pearce and Dunbar 2012). This would have enabled hominins to take advantage of the sights and sounds of vultures over longer distances.

Hadza hunter-gatherers monitor the behavior and calls of mammalian carnivores and birds, such as vultures and honeyguides (family Indicatoridae), to locate food and scavenging opportunities (O'Connell, Hawkes and Blurton 1988; Wood et al. 2014). These inter-specific relationships can be highly advantageous for humans. For example, Wood and co-workers (2014) have recently shown that the greater honeyguide bird (*Indicator indicator*) increased the rate of finding honeybee nests by 560% for Hadza men. Like modern-day hunter-gathers, spotting the circling of vultures from a safe locality would have been a low-risk, energy efficient, and potentially profitable means of locating meat for early hominins. Adaptations supporting evidence for endurance running (Bramble and Lieberman 2004; Ruxton and Wilkinson 2012) indicate that *H. erectus* could have competed with other fast running carnivores, such as ancestral dogs (genus *Canis*) and hyenas, which also used vulture signals to locate and gain early access to carcasses (Figure 1; see Holekamp, Boydston and Smale 2000; but see Bunn and Pickering 2010).

A major shift in stone-tool technology occurred at 1.76 Mya, with the emergence of bifacial tools (Lepre et al. 2011; Beyene et al. 2013). Around this time (1.7–1.5 Mya) the saber-toothed cats became extinct (Walker 1984; Turner and Anton 1998; Werdelin and Lewis 2013). These changes potentially increased the ability of hominins to access and process carcasses. The archaeological evidence suggests that hominins, living in small groups, mainly sought the red meat from carnivore kills, often leaving the marrow-laden bones for other scavengers such as vultures and hyenas (Domínguez-Rodrigo and Pickering 2003). However, when social group size was larger, hominins appear to have incorporated energy-rich bone marrow into their diet (Domínguez-Rodrigo et al. 2014).

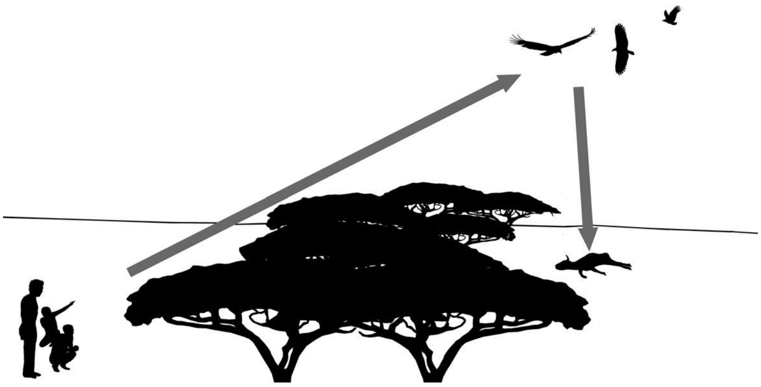

Figure 1. A graphical representation of a human group using vultures as beacons to signal food.

Bone-derived fat forms a major portion of the diet for some species of vulture. The bearded vulture (*Gypaetus barbatus*), for example, deliberately drops bones on to rocks in order to fragment or disarticulate them. This enables them to directly access the bone marrow and digest fat from bones more efficiently (Houston and Copsey 1994; Margalida 2008). Thus, relationships between hominins and vultures for access to carnivore kill sites may have varied in competitiveness according to hominin social group size and the availability of carcasses. Hominins could have also impacted the social behaviors of vultures by distributing parts of carcasses to places of safety on the landscape, which could have potentially altered the intra- and inter-specific relationships of these competitive birds (Kruuk 1967; Houston 1975; Hertel 1993; Selva and Fortuna 2007).

Monitoring the behavior of vultures could also have led early *Homo* to taste a novel energy-rich food source: cooked meat. Vultures are known to exploit fires used in the agricultural process to obtain cooked carcasses (Benson 1996) and they may use bushfires in the same way. Although use of fire is rare in the archaeological record before the Middle Pleistocene (Gowlett 2006; Alperson-Afil 2008; Shimelmitz et al. 2014), early evidence (1.5–1.0 Mya) is tentatively attributed to *H. erectus* (Gowlett and Wrangham 2013, Wameken and Rosati 2015). It has been suggested that fire may have initially been used for heat and light (Bellomo 1994), but observations of vultures scavenging cooked carcasses from bushfires may have prompted *H. erectus* to utilize naturally occurring bushfires, which would have increased the energy content of meat and plants (Wrangham et al. 1999; Gowlett and Wrangham 2013; Warneken and Rosati 2015).

The use of vultures as food signals by human groups has been investigated several times in the literature (Tappen 2001; Turner and O'Regan 2007; Lieberman et al. 2009; Ruxton and Wilkinson 2012). Conclusions suggest that scavenging opportunities would have been largely energy inefficient, unpredictable, too risky, and too rare. Based upon observations of animal behavior (including vultures) at kill sites in Tanzania, O'Connell and co-workers (1988) propose that if hominins were unable to scare off large carnivores, the amount of meat available on a carcass would have been minimal. However, dietary reconstruction of the fossilized bone remains from the nest of a bearded vulture, dated to the Pleistocene, suggest that there remained a good supply of meat for scavengers such as vultures and hominins, even after large predators had had their fill (Margalida and Marín-Arroyo 2013). Furthermore, at the end of the dry season in Africa, when large herds suffer attrition from lack of food, there can be a glut of carcasses and competition with carnivores is reduced (Blumenschine 1987; O'Connell, Hawkes and Blurton 1988). Blumenschine (1987) observed that in times of plenty, large carnivores would often become uninterested in, or abandon, meat-laden carcasses. Hominins, able to displace vultures, could have taken advantage of these periods (see O'Connell, Hawkes and Blurton 1988).

Taphonomic evidence, however, suggests that *Homo* was not just scavenging meat from abandoned carnivore kills on an opportunistic basis, but was a proficient confrontational or "power" scavenger able to displace large predators (Bunn 2001; Domínguez-Rodrigo and Pickering 2003; Bunn and Pickering 2010). Evidence of cut marks on fossilized bones indicate that hominins were defleshing parts of animals that carried substantial amounts of meat, suggesting that they had early access to intact, or nearly intact, carcasses (Domínguez-Rodrigo 1997; 1999). Would it have been possible for *H. erectus* to scare off a large predator? Contemporary humans and chimpanzees, working in groups, can seize carcasses from large carnivores by displaying with sticks and stones or making high-pitched noises (Hasegawa et al. 1983; Goodall 1986; Van der Merwe 1987). Vultures, working together, also have been known to remove a carcass from an adult cheetah (Bunn and Ezzo 1993). *Homo erectus,* with an anatomy adapted to running and throwing (Bramble and Lieberman 2004; Ruxton and Wilkinson 2012; Roach et al. 2013) and, importantly, the ability to work collaboratively like other pack animals (Walker 1984; Lewis 1997), probably presented a formidable force to a large carnivore. *Homo erectus* individuals may have preferred to passively scavenge or ambush prey when possible, but fossil evidence indicates that they also had the ability to obtain meat when the risk was much higher (Cavallo and Blumenschine 1989; Bunn and Ezzo 1993; Bunn and Pickering 2010). A more challenging task may have been to locate large "high-gain" carcasses on a regular basis throughout the year, for which they could have effectively used vultures as eyes in the skies.

The incorporation of hunting with confrontational scavenging, and possible innovations in fire and food preparation, arguably represents an evolutionary transformation in hominin feeding strategies (Brain 1981). This kind of behavioral flexibility (Potts 1996; Grove 2011; Potts 2012) may have been important in facilitating dispersal north and southwards out of the Eastern Rift, probably when conditions were harsh and resources were more uncertain (Maslin and Trauth 2009; Shultz and Maslin 2013). Following migrating ungulates and carnivores out of eastern Africa could have provided a reliable food source for dispersing hominins (Muttoni, Scardia and Kent 2013; Devès et al. 2014). Contemporary vultures and spotted hyenas in Africa routinely follow migrating animals and take advantage of their high mortality rates (Hofer and East 1993; Ogada et al. 2012). Hominins would have known that the sights and sounds of vultures and hyenas signaled the presence of carcasses or vulnerable animals. The assurance of meat would have buffered *H. erectus* against the uncertainty of an unfamiliar landscape, helping groups remain socially cohesive and increasing the chances of survival (Gamble, Gowlett and Dunbar 2011; Grove, Pearce and Dunbar 2012). Vultures may have been particularly crucial to enabling *Homo* to exploit higher latitudes where the climate was harsher, and where locating protein-laden and fat-rich food would have been critical (Rodríguez et al. 2012; Gowlett and Wrangahm 2013).

Our propositions about early hominin–vulture relationships are speculative because of the paucity of archaeological evidence at this time. Furthermore, using the behavior of contemporary species (including humans) to infer past inter-specific relationships is fraught with difficulty because of the radical decline of predators and vultures (Ogada et al. 2012). A reduction in carnivore diversity can be detected in the fossil record after 2.5 Mya, and is more pronounced after 2 Mya (Lewis 1997; Werdelin and Lewis 2013). Cerling and Hay (1986) have estimated that in the Pleistocene the average population of vultures in Africa was probably 40% higher than current populations. Today, the distribution of many carnivores in Africa, including vultures, continues to be severely affected by anthropogenic factors (Yamaguchi et al. 2004; Ogada, Keesing and Virani 2012). A history of climatic change leading to fluctuations in predator and prey populations, and differences in the behavioral profiles of extinct carnivores during the Pleistocene (Lewis 1997), mean that contemporary studies of vultures are unlikely to fully reflect the complexity of interactions between ancestral species.

Interactions between Later *Homo* Species and Vultures

Analyses of fossil assemblages indicate that ungulates and hyenas were abundant in southern France around 45 Kya (MIS 5-3; Discamps 2014). This suggests that vulture species would also have been present and thriving. At this time Neanderthals occupied Europe and anatomically modern humans (AMH) were beginning to migrate into the region (Benazzi et al. 2011; Higham et al. 2011), possibly following ungulate herds and searching for resources. By the Late Pleistocene there is strong evidence to indicate a behavioral shift in European hominin behavior. The archaeology suggests that people were not only hunting, consuming, and cooking birds, but also were using them in technology and for symbolic purposes (Cassoli and Tagliacozzo 1997; Blasco and Peris 2009; Finlayson et al. 2012; Blasco et al. 2014).

Evidence from the Middle Palaeolithic cave sites on Gibraltar, dated from 57.3 Kya, suggests that Neanderthals were probably exploiting vultures as beacons for food (Finlayson et al. 2012) and using cliff-nesting corvids, and raptors, including several vulture species, in cultural practices, possibly before the arrival of AMH in the region (Finlayson et al. 2012; Morin and Laroulandie 2012). Cut marks from stone tools, breakage patterns, burning and human teeth marks have been found on the wing bones of birds and cliff-nesting corvids and raptors that possessed dark feathers. The fact that anthropogenic activity occurs on the non-meaty parts of the birds suggests that they were not being hunted for food, but were possibly sought for other purposes, such as symbolic body adornment (Finlayson et al. 2012).

At the Middle Paleolithic site of Fumane Cave in Italy (dated to 44.8-42.2 Kya) there are further signs of Neanderthal interactions with birds, with evidence of cut marks on long bones belonging to two large species: the Eurasian black vulture (*Aegypius monachus*) and the bearded vulture (Peresani et al. 2011). Numerous modifications are evident on the wing bones, such as signs of peeling, striae, and disarticulation, indicating feather plucking and skinning. It has been suggested that the long and large feathers of vultures could have been used as a stabilizing element for hunting spears (Peresani et al. 2011).

Around 40 Kya, AMH began to move north into northwest Europe via the Danube Corridor (Higham et al. 2012), bringing an apparently more sophisticated cultural repertoire. From a site at Hohle Fels, Germany, dated to more than 35 Kya, a griffon vulture bone used to make a flute-like instrument has been recovered (Conard, Malina and Munzel 2009; Higham et al. 2012). By the Upper Paleolithic there is evidence of cooking and consuming birds, for example, at the site of Grotta Romanelli (Italy), where the assemblage includes the remains of a griffon vulture (Cassoli and Tagliacozzo 1997). The presence of cut marks on the femur and scapulae of this raptor suggests *G. fulvus* may have been part of the diet and/or a source of feathers.

Vultures continue to be evident in the Middle Bronze Age period, with their presence documented at La Starza, Italy (Albarella 1997). According to Albarella (1997), vultures were probably prized for their long feathers, which could be used in ritualistic ceremonies or as practical tools. Further evidence for the use of vulture bones as a raw material for tool production comes from the Bronze Age site of Shahr-i Sokhta, Iran (Gala and Tagliacozzo 2014). Clear-cut marks on the distal end of the ulna of the cinereous vulture (*Aegypius monachus*) suggest intentional detachment before the bones were modified into pointed tools and possibly also ornamental objects (Gala and Tagliacozzo 2014).

The archaeological evidence from the Middle and Upper Palaeolithic onwards suggests that Neanderthals and AMH were using vultures in cultural practices; for instance, using feathers in composite tools and as body adornments (Peresani et al. 2011; Finlayson et al. 2012; Morin and Laroulandie 2012), as well as eating them (Cassoli and Tagliacozzo 1997; Peresani et al. 2011). However, although most contemporary populations would not consider eating vulture meat (see Finlayson et al. 2012), indeed religious texts in both the Judeo-Christian and Muslim tradition advise against eating these birds (e.g., Leviticus 11:13) (Pullan 2012) and the Koran warns against eating birds with talons (Ali 1998), this may not reflect the behaviors of people in the deep past. Vultures are hunted for food in parts of Africa and Central India today (Koenig 2006; Ogada, Keesing and Virani 2012; R. Yosef, pers. comm.), so it is conceivable that prehistoric humans also regularly consumed them as part of their diet or as fallback foods (Marshall et al. 2009).

Vultures and Human Societies

During the Late Pleistocene and early Holocene large mammal populations were decimated in global megafaunal extinctions, which undoubtedly impacted vulture species (Hertel 1993; Bretagnolle et al. 2004; Fox-Dobb et al. 2006). In North America, possibly half the raptor species became extinct (Grayson 1977; Fox-Dobb et al. 2006). Evidence suggests that climate change, combined with human activity, played a role in these events (Barnosky et al. 2004; Sandom et al. 2014).

Once the glaciers retreated and the climate stabilized in the Holocene, opportunities arose for further cultural change (Richerson, Boyd and Bettinger 2001; Larsen 2003). Many humans continued to live as small groups of nomadic hunter-gatherers (Marlowe 2005) and the role of vultures signaling meat on the landscape is likely to have continued to be significant (Shipman 1985; O'Connell, Hawkes and Blurton 1988). Some groups, however, became reliant on domesticated cereals and animals (Zeder 2008), and vultures were no longer necessary for locating food. Vultures probably became useful in a hygienic role by removing domesticated animal debris before putrefaction (Prakash et al. 2003; Ogada, Keesing and Virani 2012; Moleón et al. 2014), which was important as populations grew denser and diseases transmission increased (Barrett et al. 1998; Larsen 2003). Vulture stomach acid is strong enough to neutralize most bacteria and many pathogens, including anthrax (Houston and Cooper 1975). Within settled communities human–vulture relationships became truly symbiotic, in exchange for access to the carcasses of domesticated animals and other food debris, vultures removed carrion quickly and efficiently, keeping humans safe by reducing the sources of contagious diseases (Markandya et al. 2008).

During the Neolithic, vultures began to be depicted in art, suggesting that they were becoming embedded in myths and religion (Russell and Düring 2006). Several human-like representations of vultures are preserved in depictions made by sedentary communities, for example at Göbekli Tepe, Turkey (~9000 BP), Çatalhöyük, Turkey (~7000 BP), and in caves such as Baja California, Mexico (~7500 BP) (Crosby 1998). Excavations at Çatalhöyük have recovered the skulls of vultures from the walls of buildings (Mellarrt 1966; Russell and McGowan 2002) and it has been proposed that some skeletal remains indicate secondary burials (Mellart 1967). Depictions on stones showing vultures hovering close to headless human figures suggest that the bodies of the dead could have been left exposed to the elements and their flesh consumed by vultures, as in the Zoroastrian tradition. These images have been used to support evidence of secondary burial of skeletal remains at Çatalhöyük (Mellaart 1967; MacQueen 1978). However, more recent analyses suggest that bodies were buried intact (Andrews, Molleson and Boz 2005). Nevertheless, the evidence indicates that vultures and other large birds, such as cranes (family Gruidae) (Russell and McGowan 2002), were used in symbolic rituals and occupied an important place in the minds and lives of the people.

As vultures are often found close to dying animals, they were thought to have prophetic abilities and powers of divination (van Dooren 2011). This included the apparent ability to foretell which armies would sustain the most losses in battle (Horapollo cited in Turner Cory 1840). Depictions of vultures following armies into battle and feeding on the vanquished have been recovered from archaeological and historic sites from ancient Sumer, Egypt, and Assyria (Mundy et al. 1992; van Dooren 2011). In ancient Egypt, vultures were believed to have positive associations (Velde 2008) and were strongly linked to rulership, appearing alongside Uraeus, the Egyptian cobra, on the burial headdresses of the kings. On the headdresses, the ornamental pose of the bird, often described a griffon vulture, but also occasionally identified as a lappet-faced vulture (*Aegyptius tracheliotus*), is positioned with the wings in a protective position (Velde 2008; Monkhouse 2012). The Egyptian goddesses Mut and Nekhbet are depicted as vultures in their hieroglyphs and are associated with femininity, motherhood, birth and death, and rulership (Velde 2008; van Dooren 2011). Nekhbet was a tutelary goddess of Upper Egypt and was represented as a woman with a vulture's head, as a vulture with the crown on her head, or occasionally as a cobra (Shaw and Nicholson 1995). The powers of these goddesses were believed to stretch beyond this world and protection on the journey into the next world would be sought by reciting the "spell for the golden vulture" described in the Egyptian *The Book of the Dead* (Faulkner 2008).

The powers the Egyptians conferred on vultures likely emerged because of the characteristics and behavior of the birds (van Dooren 2011). For example, vultures can have low sexual dimorphism (Houston 2001), which may have given the Egyptians the impression that the birds were all female and were able to reproduce without males (Velde 2008). Similarly, the Roman writer Claudius Aelianus (ca. 175 – ca. 235) wrote, "it is said that no male vulture is ever born: all vultures are female. And the birds knowing this and fearing to be left childless, take measures to produce them as follows. They fly against the south wind. If however the wind is not from the south, they open their beaks to the east wind, and the inrush of air impregnates them, and their period of gestation lasts for three years" (Aelian 2011). The long periods over which female birds tend their offspring (Koenig 2006) infer nurturing and protective qualities and commitment to motherhood (Horapollo cited in Turner Cory 1840). The fact that the birds nest in high places, often inaccessible and out of sight of people, also might have given the impression that the long flights of vultures took them to another world (Pliny the Elder cited in Bostock 1855).

Vultures were revered and incorporated also into the prehistoric cultural traditions of the Americas. Throughout the second millennium BC vultures appear to have played an important role in early religious practices in Peru. Vulture burials have been found at the central Andean site of Mina Perdida, in which birds were wrapped in cloth, with the evidence suggesting that the birds' remains were considered to be shaman transformations or ancestral spirits (Bogucki 2008). Several monuments from the Maya civilization preserved pictorial records of dancers with headdresses in the form of a vulture. The depictions are believed to be Holmul Dancers, which symbolize rulership (Looper 2009).

In Mesoamerican traditions, vultures also were associated with transformation and the life-giving properties of crops, rain, sun, fire, and light (Benson 1996). A gathering of vultures at the time of sacrifice could have symbolized the acceptance of the Gods and the prospect of good fortune (Kampen 1978), while their propensity to scavenge on carrion of animals that died during crop-burning may have fostered the mythical links to fire (Benson 1996). Benson (1996) describes the prominence of vultures in early Mesoamerican fables and the ambiguous symbolism of the birds in the peoples' perception to either provide help or cause harm. This apparent reverence for vultures in ancient cultures contrasts with the beliefs of the Greco-Roman and Judeo-Christian traditions (Velde 2008). In Greek mythology, being fed to the vultures was a punishment of the Gods (Evelyn-White 1920). The Iliad described how being eaten by vultures deprived people of their funerary rites (Homer cited in Butler 1952). In the New Testament, both Matthew (24:28) and Luke (17:37) directly associate vultures with death (Pullan 2012).

Documentary evidence, from the Egyptian era onwards, powerfully implicates vultures in providing life-giving forces, as well as in the maintenance or restoration of health. An Egyptian papyrus describes a spell to ward off illness that was recited over two vulture feathers (MacKinney 1942). A short treatise on remedies and magic based upon vulture parts, the *Epistula Vulturis*, reported to date to the time of Charlemagne, indicates that vultures were believed to hold magical, healing, and even aphrodisiac properties (van Dooren 2011). This *Epistula Vulturis* appears to have been in use at least up until the fifteenth century (MacKinney 1943), and the curative properties of vultures continued to be published into the late-nineteenth century (MacKinney 1942).

Vultures are still used today in the traditional southern African medicine "muti" (Mundy et al. 1992; Ogada, Keesing and Virani 2012), indicating that some people continue to believe these enigmatic birds hold magical powers and healing properties. Since the introduction of the state-controlled lottery in South Africa in 2000 there has been a marked increase in the demand for vultures for use in traditional medicine (Colahan 2004; McKean 2004; Van Rooyen 2004). It has been reported that smoking dried vulture brains can conjure visions to predict winning lottery numbers (The Telegraph 2009). The persecution of vultures, often by poisoning carcasses, is a huge threat to these birds in Africa (Ogada, Keesing and Virani 2012).

Human cultural traditions are being impacted also by the decimation of vultures in Asia. Hindu reverence for the cow has traditionally made the Indian subcontinent a stronghold for vultures, but the near extinction of vulture populations in recent decades is having a significant effect on the Parsi tradition (van Dooren 2011; Ogada, Keesing and Virani 2012). The Indian Parsi community, descendants of the Iranian Zoroastrians, believe that the corpse is a host of decay and must be carefully disposed of to prevent it contaminating the surroundings. The scriptures consider fire, earth, and water to be sacred elements, and cremating or burying the dead can sully these. The Parsi therefore expose their dead to wild animals and vultures. Disposal of the corpse is carried out on high stone "Towers of Silence" and it is the vultures that are primarily relied upon to quickly remove the flesh. However, the speed with which the Parsi dead are disposed of has been severely affected by the loss of 97–99% of vulture populations over the past decades (Prakash et al. 2003; Koenig 2006; Ogada, Keesing and Virani 2012). This has been attributed to poisoning by the veterinary drug Diclofenac, used to treat cattle (Yosef and Bahat 2000; Green et al. 2004; Shultz et al. 2004; Swan et al. 2006; Das et al. 2010; Camińa and Yosef 2012; Galligan et al. 2014). The population crash is also impacting the Tibetan tradition of "Sky Burials" (Ogada, Keesing and Virani 2012). The Parsi have attempted to counteract the problem by using powerful solar refactors to speed up decomposition of their dead, but these are nowhere near as effective as the vultures (van Dooren 2011; Ogada, Keesing and Virani 2012).

Vultures still play an important hygiene role in some societies by their consumption of animal carcasses (Prakash et al. 2003; Ogada, Keesing and Virani 2012; Moleón et al. 2014), refuse (Pomeroy 1975), and excrement (Negro et al. 2002). They are particularly important in many developing tropical countries where sanitary waste and carcass disposal programs may be limited or non-existent (Prakash et al. 2003). Decline in vulture numbers can lead to public health problems. In India, vultures compete with feral dogs, which often carry rabies. As vulture numbers have fallen, the numbers of feral dogs and rats have significantly increased in some localities (Pain et al. 2003; Prakash et al. 2003; Markandya et al. 2008). The loss of vultures has consequences for society. Aside from the direct impact on culture and potential loss of ancient traditions, there are huge costs involved in ensuring public health via refuse and carcass disposal and providing healthcare to treat the rise in diseases and injuries, such as rabies from infected dog bites (Moleón et al. 2014). The estimated cost of dealing with rabies in India, following the decimation of vulture numbers, is nearly $1.5 billion per year (Markandya et al. 2008).

In many modern societies, attitudes toward the natural world are shaped by multiple complex factors such as genetics, parents, direct experience, and the media (Ballouard, Brischoux and Bonnet 2011). In western societies, often the first experiences we have of vultures come from the media. Vultures have featured in several well-known children's animated movies, which overwhelmingly reinforce the stereotypical views of the birds. The vultures in these films are usually peripheral characters and are often portrayed as scruffy, stupid, sneaky, bullying or evil, and are frequently seen congregating in a menacing manner (e.g., Katschke 1994).

More recently, popular concepts of vultures have also become embedded in contemporary language, with vultures being linked to financial sectors that clear-up after bankruptcies, or that prey on failing companies with bad debt or weak assets (Rosenberg 2000; Schultze and Lewis 2012). These examples of cultural paradigms elicit emotional states that serve to strengthen the negativity surrounding vultures. Unsurprisingly, these birds are conspicuously absent in other aspects of western culture, such as advertising, that uses positive imagery to conjure emotions linked to western ideals such as power, success, beauty, and cleanliness.

Vultures undoubtedly occupy a niche that many humans associate with disgust and fear (Houston and Cooper 1975; Negro et al. 2002). These emotions are important evolutionary adaptations that have evolved to keep us safe by avoiding dangerous situations and harmful pathogens (Prokop and Fančovičová 2013; Lorenz, Libarkin and Ording 2014). However, many westerners live in societies that have reduced the risk of contracting life-threatening diseases (e.g., via sanitation, public health) and minimized the danger of being harmed by dangerous animals. This disconnectedness from the biological environment appears to be associated with reduced knowledge of local biodiversity and may also alter public concepts of many potentially dangerous (usually exotic) animals (Ballouard, Brischoux and Bonnet 2011). For example, despite an awareness of the dangers associated with large, wild animals, we tend to retain a positive view of them. This is reflected in the ubiquity of these animals in retail and the media (e.g., lions, tigers, elephants).

In stark contrast, many "unattractive" harmless, smaller animals do not have favorable public images, even though they may play an important role in the maintenance of ecosystems. Insects are a good example. Humans exhibit strong disgust and fear responses to arthropods (although butterflies and bees may be different) (Gerdes, Uhl and Alpers 2009; Prokop and Fančovičová 2013; Lorenz, Libarkin and Ording 2014). It is possible that, like insects, carrion-eating, coprophagous vultures (Negro et al. 2002) elicit emotions in humans that align with the construct of pathogen disgust (Lorenz, Libarkin and Ording 2014), although this remains to be tested.

Understanding the mechanisms that underpin public perceptions of wildlife is important because the way we feel about animals can have an impact on the success of conservation programs (Ducarme, Luque and Courchamp 2013). Some conservation programs do not need to improve the image of the animal under threat because their public identity is already iconic (e.g., pandas, elephants). Many of these animals are labeled as "charismatic" species, despite the lack of consensus on the definition (Ducarme, Luque and Courchamp 2013). The "charismatic" label may be particularly important for threatened species, as it has been shown to influence donors' willingness to financially support conservation (Ducarme, Luque and Courchamp 2013). It therefore seems somewhat unfair that "non-charismatic" vultures, which have formed a mutualistic relationship with humans through evolution and have been revered by many cultures through much of history and to the present day (e.g., the Parsi), are blighted by such strong, negative emotions and poor cultural stereotypes.

Vultures Threatened by Humans

Vulture populations appear to have been significantly declining for over 100 years, so estimating the impact of more recent threats to the ecology and economy is difficult (Moleón et al. 2014), but human activities have impacted vultures probably since the Early Pleistocene (Werdelin and Lewis 2013). More recent anthropogenic actions, however, are on a scale that leaves vulture populations unable to recover without intervention. The impact of Diclofenac on vultures is one of the most extreme examples of man's effect on the birds of prey (Oaks et al. 2004; Shultz et al. 2004; Naidoo et al. 2009). The drug is harmless to humans and cattle, but in vultures it causes kidney failure and visceral gout; a condition in which uric acid is deposited on or in the internal organs (Oaks et al. 2004; Shultz et al. 2004). Manufacturing Diclofenac was halted in India, Pakistan, and Nepal in 2006 (Ogada, Keesing and Virani 2012) and its use has been banned in India (Cuthbert et al. 2011; Prakash et al. 2012), but it remains in use in other countries (e.g., Spain; Margalida et al. 2014).

Across rural West Africa vultures have declined in number by 95% in the past 40 years (Koenig 2006) and continue to come under threat from a wide range of factors, all of which are connected to human action (Ogada, Keesing and Virani 2012). In parts of South Asia, direct persecution of vultures, combined with the loss of wild ungulates through hunting, which has reduced the number of non-medicated carcasses, have drastically impacted vulture populations (Pain 2003). In Europe, recent changes in hygiene laws, which came into effect to protect human health after the Bovine Spongiform Encephalopathy outbreak in 2001 (Margalida et al. 2012), have prevented animal carcasses from being left in the landscape, removing a vital food source for vultures (Ogada, Keesing and Virani 2012).

The problem is global; human persecution, urban expansion, habitat destruction, intensification of agriculture, pesticides, power lines, wind turbines, and poisoning have all contributed to the radical decline in vulture populations (Koenig 2006; Ogada, Keesing and Virani 2012; Moleón et al. 2014). Koenig (2006) cites a case in Africa in which 187 vultures and four hyenas died from feeding on one poisoned cow carcass. Farmers poison carcasses to get rid of pests such as hyenas and jackals (family Canidae) (Koenig 2006), yet this only exacerbates the problem. Poisoned carcasses kill vultures; reduced numbers of vultures lead to decreased rates of carcass decomposition, which increases the presence of other scavengers (Ogada et al. 2012). Ogada and co-workers (2012) found that when vultures were absent at carcasses in central Kenya, the presence of spotted hyenas (*Crocuta crocuta*) increased by 87% and striped hyenas (*Hyaena hyaena*) by 100%.

Slow reproductive rates make it difficult for vultures to recover when populations are reduced (van Dooren 2011; Ogada, Keesing and Virani 2012). Their longevity also makes them vulnerable to the bioaccumulation of toxins, which impacts reproductive rate (Gangoso, Alvarez-Lioret and Rodriguez-Navarro 2009). For example, the widespread use of pesticides, such as DDT, are known to thin the shells of many birds of prey, which can be devastating for vultures that are monogamous and only lay one or two eggs per year (Ratcliffe 1967; Newton et al. 1982; Newton, Bogan and Rothery 1986).

Vultures are top carnivores (Koenig 2006; Ogada, Keesing and Virani 2012) and their role in the world not only signals food to animals, but signals the health of regional ecologies. Their absence at large carcasses affects community structure and the abundance and behavior of other scavengers (Selva and Fortuna 2007; Ogada et al. 2012). Vultures also play an important role in the efficiency with which nutrients are transferred through food webs (De Vault, Rhodes and Shivik 2003; Wilson and Wolkovich 2011). In Kenya, the reduction in vulture numbers has led to a significant reduction in decomposition rates of carcasses (Ogada et al. 2012), which increases the threat of disease transmission and slows the recycling flow of nutrients.

Vultures and Humans: The Story Continues

In Europe and North America, historical declines in vulture populations appear to have stabilized, but in other parts of the world vulture numbers remain highly threatened (Ogada, Keesing and Virani 2012). As Moleón and co-workers (2014) point out, when the decimation of vulture populations is linked to one problem, such as Diclofenac use in Asia, it is relatively simple to tackle, but when the causes are complex, varied, and interwoven with longstanding cultural practices, as in Africa, the task is much more challenging. Fortunately, the decimation of vultures in Asia has been a wake-up call to researchers, conservationists, and government agencies to better understand threats to vulture abundance and behavioral ecology (Koenig 2006).

New efforts to help and conserve these wonderful birds of prey offer some hope for the future. Some of these changes are straightforward: insulating power lines (Van Rooyen 2004; Koenig 2006), tagging and monitoring (Bögel 2006; Margalida et al. 2008; García-Ripollés, López-López and Urios 2011), switching to less harmful veterinary drugs (Cuthbert et al. 2011), vulture feeding stations (Bahat 2001; Piper 2006; Becker et al. 2009; 2010), and leaving carcasses in the landscape (Margalida et al. 2012). Others require more funding and longer-term investment. For example, education, conservation and research programs should ideally monitor vulture populations over generations and document their impact on species diversity, the regional ecology and economy, as well as human welfare (Koenig 2006; Becker et al. 2009; 2010; Ogada, Keesing and Virani 2012; Moleón et al. 2014).

Despite their "non-charismatic" status, there have already been some positive outcomes in vulture conservation, with several examples of captive breeding programs enabling vultures to be successfully reintroduced back to the wild: the Californian Condor in the USA, the griffon vulture in the Massif Central (France), and the bearded vulture in the French Alps (Houston 2006; Terrasse 2006). However, careful monitoring of the bearded vulture populations since their reintroduction in 1986 has shown that over half the vultures continue to be killed by poisoning or shooting (Margalida et al. 2008; van Dooren 2011; Horowitz et al. 2014). This example warns against becoming complacent about conservation schemes and emphasizes the importance of long-term monitoring, education (Terrasse 2006), and public awareness (e.g., International Vulture Awareness Day).

Conclusion

In this work we have suggested how vultures, exploited as beacons for high quality food, can be considered central to one of the most ancient relationships between *Homo* species and birds. This relationship was likely important in helping early hominins locate meat and could have facilitated their dispersals out of Africa. The importance of vultures to archaic and modern human species is indicated by their incorporation into culture as aspects of the symbolic universe. With the advent of sedentism, the mythical and prophetic nature of vultures was embedded further into cultural practices. In recent times, vulture populations have gradually declined, but this has accelerated in the past half century to a point of near extinction for many species (IUCN 2005).

Throughout history vultures juxtapose between positive and negative concepts: compassionate and cruel, terrifying and protective, life and death, harm and healing (Benson 1996; Velde 2008; van Dooren 2011). Even early hominins, alerted by vultures to the presence of life-giving food, potentially faced death when scavenging from large predators. Concepts of what vultures represent, however, have become skewed. Today the popular western concept of vultures is wholeheartedly negative and has probably fostered our ambivalent attitude toward their plight.

There is no doubt that vultures are fundamental to maintaining our ecosystem and should therefore be protected. Loss of vultures from their habitats will impact animal diversity and likely have widespread ramifications for ecosystems. As ecologists and conservationists, we already feel that vultures are "charismatic" animals that deserve a comprehensive, global conservation effort. It is therefore our duty, not only as scientists, but also as human beings, to educate people about these special birds to ensure their survival for generations to come. However, without commitment by governments to funding vulture conservation programs over the long-term, the ability to preserve many species may be limited (Ogada, Keesing and Virani 2012). It is therefore sobering to think that despite our close relationship with vultures over most of human evolution, this long relationship may soon end due to the actions of humans.

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