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The natural history of scavenging in vertebrates

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Abstract

Scavengers existed in the past and they exist now. Often under appreciated. Three main habitat types considered: land, air and sea. Different drivers in these areas. Review looks at these

Introduction

Historically, scavengers have not been viewed as the most charismatic of animals. This may go some way to explaining the gap in our knowledge of the prevalence of this behaviour. Consider Professor Sanborn Tenney writing in 1877 for The American Naturalist who had this to say about one well known group, "Prominent among the mammalian scavengers are the hyenas, the ugliest in their general appearance of all the flesh eaters." He contrasts these with "nobler kinds" of carnivores such as lions and tigers. Even aside from our own subjective biases, scavenging is a difficult behaviour to detect after the fact. Without catching a carnivore in the act of killing we are left to infer how the prey was killed. Some simple heuristics can inform us, for instance, in cases where the prey item was simply too large to have been killed by the ostensible predator (Pobiner 2008). But clearly, a scavenger doesn't only feed on animals too big for it to have hunted. The obvious lack of direct behavioural data compounds the difficulty of discerning scavenging among extinct forms. Indeed, a single species of dinosaur notwithstanding, a synthesis describing the natural history of scavengers is absent from the literature. Fortunately, research in this area is on the rise. As a result we are now beginning to realise the extent of this behaviour such that, "in some ecosystems, vertebrates have been documented to assimilate as much as 90% of the available carrion" (Benbow et al. 2015). Even Tenney's noble big cats are now known to take in a significant portion of carrion in their diet where some lion populations get over 50% of their meat from carcasses. A suite of methods have been used to discern the most suitable morphologies, physiologies and environments for a scavenging lifestyle to prosper. It is our aim in this review to employ these methods to gain an understanding of scavengers past and present.

The chief hurdle to scavenging is finding a sufficient quantity of food, the occurence of which is difficult to predict in space and time. The idea of scrounging from predator kills is undermined from studies showing that in the majority of ecosystems more animals die from disease and starvation than predation (Benbow et al. 2015). Thus, any animal existing as a scavenger must maximise its detection capabilities and minimise its locomotory costs (Ruxton and Houston 2004b). The habitat must also be productive enough to sustain an animal biomass that will eventually produce carcasses. It is recognised that scavengers keep energy flows at a higher trophic level in food webs than decomposers because they consume relatively more carrion (DeVault et al. 2003).

Aerial Scavengers

Vultures represent the best known scavengers on Earth. These birds consist of two convergent groups, from the old and the new world and represent the only example of obligate vertebrate scavengers today. Given their unique position, they have been extensively studied to determine what adaptations they possess that allows them to so flourish in this niche. As such, we can begin by exploring the adapdations and the environments of vultures to draw comparisons with other scavenging species and *their* environments.

Species capable of flight have effectively added an extra spatial dimension, i.e. the vertical component, to their sensory environment over land animals. This allows them to look down on a landscape where they are unencumbered by obstacles that would obstruct the view of a terrestrial scavenger. Such an ability has obvious benefits in detecting carrion. Vultures are known to have impressive visual acuity with one estimate indicating Lappet-faced Vultures (*Torgos tracheliotus*) are capable of detecting a 2 metre carcass over 10 km away (Spiegel et al. 2013). We know that many birds exist as facultative scavengers; storks, eagles, corvids, are all known to take substantial quantities of carrion in their diet. And eagles in particular are known to have highly developed visual abilities. It follows from this that the evolution of flight allowed aerial animals to detect far more carrion than their terrestrial counterparts.

Moreover, having a panoramic view means being able to gather a wealth of information from other foragers, be they conspecifics or other species. Again, returing to vultures, the genus *Gyps* consists of highly social and colonially nesting species. These behaviours allow them forage far more efficiently because one bird can scrounge information on the location of food from another successful forager.

Flight is also cheaper means of locomotion than running (Tucker 1975). This advantage can be extended further in larger species by engaging in soaring instead of flapping flight, which is even cheaper still (approximately twice BMR) (Hedenstrom 1993). The advantages this confers are clear from the information we have on the enormous foraging ranges of some seabirds and accipiters. Clearly, it would be pointless to have incredible detection abilites and not have a cost efficient movement to benefit from it.

Avian flight originates in the Jurassic Period, conincident with the fossils of *Archaeopteryx lithographica* so many of these benefits would have been realised from that point on for carnivorous birds. However, vertebrate flight is much older than this where pterosaurs predate bird origins by a considerable margin in the Triassic Period. Scavenging in this diverse group has been hypothesied many times before. Certain clades of these animals could reach enormous sizes (e.g. Azhdarchids with wingspans of 11 metres) and look to have engaged in soaring flight. Although Witton and Naish (2008) argued that neck inflexibility and straight, rather than hooked jaw morphology points against their existing as *obligate* scavengers, Azhdarchid terrestrial proficency indicates they would have been comfortable foraging on the ground. Indeed, extant Marabou Storks have a comparable morphology and are noted facultative scavengers so it is reasonable to believe that certain pterosaurs behaved similarly.

Large body size confers substantial dominance benefits (Ruxton and Houston 2004b). Thus, we would expect scavengers to have this trait selected for even in the case of weight-constrained fliers. Cinereous Vultures (*Aegypius monachus*) and condors (*Vultur gryphus*, *Gymnogyps californianus*) all have body masses that can exceed 10 kg and represent some of the heaviest bird species capable of flight (Ferguson-Lees and Christie 2001, Donázar et al. 2002). And as we have noted the Azhdarchid pterosaurs were far bigger again, with estimated body masses of around 80 kg.

The only other vertebrate group capable of powered flight are the bats where scavenging has not been recorded to our knowledge. Their visual acuity is famously poor and echolocation does not lend itself to discovering immobile carrion. Their small size and poor terrestrial ability would also count against them at a carcass. The bat fossil record is notoriously poor owing to their fragile skeletons so we are unable to determine if extinct species were more suited to this lifestyle.

Vertebrate scavengers in general are responsible for the dispersal of nutrients. Consider the diversity of animals that can end up feeding at the carcass of an elephant. Here we have an incredibly dense and nutrient rich patch that ends up being distributed widely. Thus, in an ecological context, the evolution of flight coupled with the ability to scavenge resulted in a world with a far more widely distributed nutrient landscape. In the absence of vertebrate scavengers, invertebrates and microorganisms would consume the carcass in-situ or at least distribute the constituent nutrients over a much shorter range.

Terrestrial Scavengers

A simplificaiton of terrestrial scavengers is one of them existing in a two-dimensional plane while foraging for carrion directly. They can detect carcasses at a range that is defined by the radius of their sensory organs, usually the visual and olfactory senses. As a consequence, they have a much more restricted view of the landscape than do aerial foragers. No contemporary terrestrial vertebrate exists as an obligate scavenger but most if not all are facultative scavengers to some extent. Ruxton and Houston (2004b) offer a reason for this in that the traits that allow for vultures to exist as scavengers undermined their ability to hunt but that the same forces have not prevented mammals from doing so. The same authors in a theoretical study do concede that "a 1 tonne mammal or reptile, in an ecosystem yielding carrion at densities similar to the current Serengeti, could have met its energy requirements if it could detect carrion over a distance of the order of 400–500 m."(Ruxton and Houston 2004b).

Terrestrial scavenging in the mammals is probably best known in an African context where hyenas, jackals and lions all take sizable proportions of carrion in their diet. In the spotted hyena (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*) and brown hyena (*Hyaena brunnea*) it can be as high as 99% (Benbow et al. 2015). Therefore, we can again use these species as our efficient terrestrial scavengers to compare with other forms.

Similar to vultures they have well developed sensory organs, particularly in olfaction whereby they can detect a rotting carcass 2 km downwind. They have a characteristic "rocking horse gait" which allows them to cover great distances efficiently. The bone crushing ability of hyenas reveals another useful scavenger trait. Since carrion is not dispatched directly, often the most easily accessible and choicest components of the carcass will be missing or, if present, will be fought over. Being able to extract nutrients from remnants gives the scavenger a great advantage. Osteophagy is known across a range of terrestrial carnivores. Some fat-rich mammalian bones have an energy density (6.7 kJ/g) comparable with that of muscle tissue, making skeletal remains an enticing resource (Brown 1989). This ability reached its zenith among hyenas with the evolution of the 110 kg *Pachycrocuta brevirostris* during the Pliocene (Palmqvist et al. 2011). The ability to process bone means a carcass fed on by hyenas will be reduced to nothing, whereas the skeleton will remain in carrion attended by species restriced to feeding on the flesh.

Many of these adapations to scavenging are found in the other major extant terrestrial mammalian carnviores, the bears, dogs and cats to a greater or lesser extent. Though the specific mix of features realised in hyenas suggest this is the model organism for terrestrial scavenging among mammals in the past. Indeed, the bone-crushing dogs that evolved during the Oligocene (subfamily Borophaginae) have been compared to hyenas in terms of their feeding ecology (Van Valkenburgh et al. 2003, Martín-Serra et al. 2016). Interestingly such comparisons have given insight into the feeding ecology of early hominins who, for instance, had the ability to craft tools for breaking open bones (Hone and Rauhut 2010, Blasco et al. 2014).

By contrast, a successful reptilian scavenger requires a far different set of adapations. Modern forms are ectothermic, limiting their activity periods. This is exacerbated by the sprawling gait seen in lizards which results in Carrier's Constraint such that the animal can't move and breathe at the same time because the lateral movements impedes its lungs. This manifests itself in aspects such as maximum sustainable speed where an equivalent mammal has a six to seven fold increase (Ruben 1995). A lower metabolism does give reptiles an advantage however, in that over the course of a year their food requirements can be 30 times smaller than an endotherm of equal size (Nagy 2005). Any adaptations that reduce energetic costs are likely to be selected in scavengers. DeVault and Krochmal (2002) suggest this is an avenue for scavenging in snakes because they "exhibit exceedingly low maintenance metabolisms, and most can survive on a few scant feedings per year. It is, therefore, possible for snakes to rely largely on infrequent, less energy-rich meals." In the same review the authors found occurrences of scavenging spread across five families of snakes and stated that this behaviour is "far more common than currently acknowledged."(DeVault and Krochmal 2002).

Unsurprisingly, given their enduring appeal, the prevalence of scavenging has been explored in the carnivorous, theropod dinosaurs. These animals ranged from the chicken-sized to the whale-sized all of which were bipedal. They are quite alien to anything we know today which restricts our ability to understand their ecology far more so than extinct mammals (Weishampel et al. 2004). Of relevance, are the questions that still persist about their metabolism (Grady et al. 2014) and sensory perception. We do know that they walked with the erect gait of mammals or birds rather than the sprawling gait of lizards and that they were most likely facultative scavengers (DePalma et al. 2013). Much work has focused on the existence of the behaviour in *Tyrannosaurus rex* (Ruxton and Houston 2003, Carbone et al. 2011) but a recent energetics study investigated the likely prevelance of scavenging across a range of body sizes. In it the authors demonstrated that species of intermediate body masses (approx. 500 kg) would have gained the most benefit from scavenging. This was the result of gut capacity limitations and the effects of competition at the carcass. At the larger extreme this owes to the fact that gut capacity doesn't scale isometrically with body mass so the benefits of greater mass level off; there's only so much food an individual can consume at a single sitting. For the smaller species, larger competitors would have prevented their access to carrion.

As we discussed for the case of Cenozoic carnivores, osteophagy could be extremely beneficial to a scavenger. In Mesozoic systems some extremely large theropod dinosaurs had a morphology which suggests an ability to process bone e.g. the robust skull and dentition of *T rex*. There is direct evidence that *T.rex* did this in the form of distinctive wear marks on its tooth apices (Farlow and Brinkman 1994, Schubert and Ungar 2005) and the presence of bone fragments in its coprolites (Chin et al. 1998). The animal also had an enormous bite force, with one estimate putting it at 57000 Newtons (Bates and Falkingham 2012). This is noted as being powerful enough to break open skeletal material (Rayfield et al. 2001). Osteophagy may have been even more viable during this era because the body mass distribution of herbviores tended to be skewed towards larger sizes (O'Gorman and Hone 2012). When we couple this with the fact that skeletal mass scales greater than linearly with body mass (Prange et al. 1979) there would have been a lot of bone material to consume in the environment provided an animal had the biology to process it (Chure and Fiorillo 1997).

Evidence of vertebrate scavenging dates back to the early Permian approximately 300

MYA (Reisz and Tsuji 2006).

Aquatic Scavengers

An aquatic environment presents challenges for direct observational studies and so, similar to the approaches involving extinct species, much work has approached the question of scavenging propensity from an energetics perspective. The existence of an obligate scavenger in a marine setting is uncertain (Britton and Morton 1994, Smith and Baco 2003, Ruxton and Houston 2004a, Ruxton and Bailey 2005). Carrion in this environment is produced by marine organisms when their carcasses descend to the sea floor. In this low-light environment detection distances are far lower (< 100 m) than they would be in the air. As such, animals detect resources through chemo- and mechanoreception more so than through vision (Ruxton and Houston 2004a). However, water is a medium that is conducive to low-cost movement (Tucker 1975) and so may be able to support an obligate scavenging fish (Ruxton and Houston 2004a, Ruxton and Bailey 2005). Benbow et al. (2015) do note that "some benthic scavengers (e.g., hagfish: family Myxinidae) rely on necrophagy for a large portion of their diet and may indeed be obligate scavengers".

Extant aquatic snakes are deemed as having the most suitable physiology and environment for scavenging. A hypothesis put forth by (SAZIMA and Strüssmann 1990) argued that chemical gradients in water would allow for a relatively easier detection of carrion. This gained some support from DeVault and Krochmal (2002), who found a preponderence of aquatic snake species in their review of this behaviour.

The presence of occasional bounties of carrion in the form of whale falls has led some researchers to investigate if a scavenger could survive by seeking out these remains exclusively. Ruxton and Bailey (2005) argued that although this is energetically feasible it’s ecologically unlikely. Any animal that could seek out such whale carcasses is unlikely to have ignored other types of carrion. Although no aquatic species have ever exceeded the size of whales, some enormous animals have evolved in this environment before the evolution of whales, including *Leedsichthys*, a bony fish from the Jurassic Period, that weighed in excess of 20 tonnes. Thus, the energetic feasiblity of a marine scavenger has a long history.

As with the aerial and terrestrial enviornments we have evidence of facultative scavenging among extinct, aquatic species. For example, the remains of a mosasaur and a terrestrial hadrosaur were discovered with embedded teeth from a Cretaceous shark *Squalicorax* (Schwimmer et al. 1997). As well as a likely instance of scavenging between a 4-million-year-old white shark (*Carcharodon*) and mysticete whale from Peru (Ehret et al. 2009).

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