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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.

1 Aerial Scavengers

Vultures represent the best known scavengers on Earth. These birds consist of two convergent groups, old world and new world vultures 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 (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. Indeed, 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 (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 an ability of 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.

2 Terrestrial Scavengers

Terrestrial scavengers can be thought of as 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 carnivorous vertebrates are facultative scavenging behaviour to some extent. Terrstrial 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 case of the spotted hyena (*Crocuta crocuta*) it can be as high as 99% (Benbow et al. 2015). We can again use this species as our efficient terrestrial scavenger to compare with other species.

Similar to vultures they have well developed sensory organs, particularly in olfcation whereby they can detect a rotting carcass 2 km downwind. They have a characteristic "rocking horse gait" which allows them to cover great distances. "Apart from being an important water-conservation strategy, nocturnal behavior may have evolved in the Hyaenidae as a means of reducing competition with the other dominant scavengers in African ecosystems, the vultures, which are exclusivly diurnal (Houston 1979)" Carnivore Behavior, Ecology, and Evolution By John L. Gittleman

Most if not all carnivorous vertebrates are facultative scavenging behaviour to some extant. It is recognised that scavengers have an important role in keeping energy flows at a higher trophic level in food webs than decomposers because they consume relatively more carrion (DeVault et al. 2003). Scavengers also provide useful ecosystem services by acting as barriers to the spread of disease by quickly consuming rotting carcasses which have often died from illness (Ogada et al. 2012). Despite this, scavengers are a seriously understudied group (Sekercioglu 2006, Selva and Fortuna 2007, Wilson and Wolkovich 2011). DeVault et al. (2003) propose that this is due to both human disgust at carrion itself and the difficulty in determining if an ingested prey item was killed or scavenged. The latter point means that studying the natural history of this behaviour is particularly problematic. Indeed, even data on the proportion of carrion in the diet of extant species are sorely lacking (Benbow et al. 2015).

"Indeed, in some ecosystems, vertebrates have been documented to assimilate as much as 90% of the available carrion"(Benbow et al. 2015).

The limitations in studying scavenging in extant species are even bigger in extinct species and past systems since the obvious lack of available direct behavioural data (CITE) This means indirect observations in the fossil record and other approaches such as energetics must be used to infer these behaviours. One avenue to infer scavenging from palaeontological data can be achieved by determining if a prey item was simply too big for the carnivore to have tackled in cases where tooth marks are found (Pobiner 2008). Comparative analysis can also allow us to ascertain which morphologies and physiologies are likely to have been found in scavenging species in the past (Ruxton and Houston 2004b). The development of indirect measures of scavenging in palaeontology can in turn be applied to current scavenging systems that also suffer from a lack of observational data.

In this review we collate methods (could this be another way of structuring it, just an idea) and research form palaeontology relating to scavenging behaviour and show that ignore this literature would be a missed opportunity for understanding extant scavenging.

Our review is divided up into three sections, namely the land, air and sea. These are then subdivided into three geological eras the Cenozoic, Mesozoic and Palaeozoic. Each of these environments has a distinct phyiscal character that affects how a species forages for food which has obvious relevance for an animal searching for carrion. However, there is some commonality to a scavenger's environment and the problems in finding food that one would encounter. Notably, the resource environment of a scavenger is a patchily distributed one, because it is difficult to predict both when and where a carcass is produced. As a result of this, any animal existing as a scavenger must maximise its detection capabilities and minimise its locomotory costs (Ruxton and Houston 2004b). Exploring which groups are likely to have moved towards these traits and thus existed as sccavengers over palaeontological time forms the basis of this work.

3 Terrestrial Scavengers

As noted above the ease with which natural selection pushes an animal towards the optima of cheap locomotion and large detection capabilities is dependent on the environment the species is in. Land-based scavengers can be thought of as existing in a 2-dimensional plane while foraging for carrion directly. The range at which they can detect carcasses is thus defined by the radius of their sensory organs, usually the visual and olfactory senses.

Large body size confers many advantages to a scavenger. It grants an animal competitive benefits against other species at a carcass, it allows for some resistance to starvation because of greater fat stores and it often means the sensory organs are elevated giving a higher likelihood of discovering food (Farlow 1994).

Cenozoic

Among terrestrial African carnivores, hyenas, jackals, lions and leopards all take sizable proportions of carrion in their diet. In the case of the spotted hyena (*Crocuta crocuta*) it can be as high as 99% (Benbow et al. 2015). Yet, no contemporary terrestrial vertebrate exists as an obligate scavenger. The selective pressures that push mammals and reptiles towards scavenging do not seem to undermine their ability to hunt, perhaps explaining the absence of obligate scavengers in these groups (Ruxton and Houston 2004b).

There is a long running debate on the tendency of human ancestors to scavenge. Some recent studies have found "that passive scavenging from abandoned larger felid kills could have been a high-yield, though potentially dangerous, foraging strategy for early hominins even without considering within-bone nutrients" (Pobiner 2015).

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). Hyenas have a bite force capable of breaking open bones and early hominins had the ability to craft tools for this purpose (Hone and Rauhut 2010, Blasco et al. 2014). In light of this, the skeletal remains of carrion may act as trove of food to carnivores who can access it.

Ruxton and Houston (2004b) in a theoretical study suggested 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."

A review by DeVault and Krochmal (2002) found occurrences of scavenging spread across five families of snakes and states that this behaviour is "far more common than currently acknowledged."

Mesozoic

In a recent publication a modelling approach found that theropods between 27 kg and 1044 kg would have gained a significant energetic advantage over individuals at both the small and large extremes of theropod body mass through their scavenging efficiency. This humped pattern is the result of the disparity between the scaling of energetic cost which scales according to an exponent of 0.91 and energy input that scales according to a cubic polynomial that initially scales according to an exponent of 1.07 but plateaus after 1000kg. The polynomial behaviour of energy input is itself the result of the limitations imposed by gut capacity and the overall availability of carcasses after competition.

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 *Tyrannosaurus 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 bones to consume in the environment provided an animal had the biology to process it.

Allosaurus tooth marks on a hadrosaur in the Late Jurassic (Chure and Fiorillo 1997). Late Triassic scavenging on a prosauropod by basal carnivorous archosaurs (Hungerbühler 1998).

Palaeozoic

Synapsids Sprawling gait

Species capable of flight have effectively added an extra spatial dimension, i.e. the vertical component, to their sensory environment. This allows them to look down on a landscape where they are unencumbered by obstacles that would obstruct the view of a terrestrial scavenger. Moreover, flight is a cheaper means of locomotion than running (Tucker 1975). Thus, it appear that would-be scavengers have a distinct advantage by taking flight.

Birds are the dominant vertebrate fliers today and include the best known scavengers on Earth, the vultures. These birds consist of two convergent groups, old world and new world vultures and represent the only example of obligate vertebrate scavengers. They have a suite of adaptations that allow them to flourish in this niche. Vultures extend the energetic advantage of flight further by engaging in soaring instead of flapping flight, which is even cheaper (Hedenstrom 1993). Their efficiency is illustrated by cases of predators like bears and wolves benefiting by taking more carrion in their diet in areas bereft of vultures through competitive release (DeVault et al. 2003). In flight, birds possess a huge advantage over any terrestrial obligate scavenger. Flight affords them the ability to range over a much larger area and detect carrion from an elevated vantage point. Pennycuick (1972) conservatively estimated that a Gyps vulture could identify activity at a carcass 4 km away.

Many other bird species take a significant amount of carrion in their diet notably the eagles, storks and corvids. Although, none of them are obligate scavengers. By contrast with terrestrial species, the traits that render a bird adept at scavenging do undermine its ability to function as an effective predator (DeVault et al. 2003).

The ability to lower BMR at night is reported in some *Gyps* vultures.

In ancient ecosystems, the volant pterosaurs have also been postulated as existing in a vulture-like niche (Witton and Naish 2008). Certain clades of these animals could reach enormous sizes (e.g. Azhdarchids) and look to have engaged in soaring flight. However, the inflexibility of their necks and straight, rather than hooked jaw morphology argues against their existing as obligate scavengers (Witton and Naish 2008). As yet, no one has ever attempted an energetics approach for this group which is likely due to the many uncertainties over their biology (Witton and Habib 2010).

The absence of flying vertebrates in the Palaeozoic may have permitted terrestrial forms to take in a higher proportion of carrion in their diet.

4 Aquatic Scavengers

The existence of an obligate scavenger in a marine setting also remains hypothetical (Britton and Morton 1994, Smith and Baco 2003, Ruxton and Houston 2004a, Ruxton and Bailey 2005). Carrion in this environment is produced by dead flesh and other marine organisms when their carcasses descend to the sea floor. This low-light environment means animals detect resources through chemo- and mechanoreception (Ruxton and Houston 2004a). Detection distances are far lower than they would be in the air (< 100 m) as a result. However, water is a medium that is conducive to low-cost movement (Tucker 1975) and so may be able to support a small obligate scavenging fish (Ruxton and Houston 2004a, Ruxton and Bailey 2005). Although, for the time being this remains conjectural.

"although some benthic scavengers (e.g., hagfish: family Myxinidae) rely on necrophagy for a large portion of their diet and may indeed be obligate scavengers" (Benbow et al. 2015)

Cenozoic

A likely instance of scavenging between a 4-million-year-old white shark (*Carcharodon*) and mysticete whale from Peru (Ehret et al. 2009). Bite marks on early Holocene Tursiops truncatus fossils from the North Sea indicate scavenging by rays (Chondrichthyes, Rajidae) (van Netten and Reumer 2009). Possible scavenging on a juvenile fur seal from the Late Neogene (Boessenecker and Perry 2011).

Mesozoic

Evidence of scavenging in a Cretaceous shark species *Squalicorax* whereby remains of a mosasaur and a hadrosaur were discovered with embedded shark teeth (Schwimmer et al.

1997).

Palaeozoic

Evolution of sharks, known scavengers. Evidence of vertebrate scavenging dates back to the early Permian approximately 300 MYA (Reisz and Tsuji 2006).

Results

Discussion

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