Running title: Scavenging in vertebrates
Number of words: ∼9999

Date of submission: April 26, 2016

A Recipe for Scavenging - the natural history of a behaviour

Adam Kane, Kevin Healy, Thomas Guillerme, Graeme Ruxton, & Andrew Jackson.

1. *A. Kane (adam.kane@ucc.ie), University College Cork, Cooperage Building, School of Biological Earth and Environmental Sciences, Cork, Ireland.*
2. *K. Healy and A.L. Jackson, Trinity College Dublin, Department of Zoology, School of Natural Sciences, Dublin 2, Ireland; Trinity Centre for Biodiversity Research, Trinity College Dublin, Dublin 2, Ireland.*
3. *T. Guillerme, Imperial College London, Silwood Park Campus, Department of Life Sciences, Buckhurst Road, Ascot SL5 7PY, United Kingdom.*
4. *G. Ruxton, School of Biology, Sir Harold Mitchell Building, Greenside Place, St Andrews, KY16 9TH, United Kingdom.*

Abstract

Despite its prevalence, scavenging is a difficult behaviour to observe in modern day carnivores and impossible to study directly in extinct species. Yet, there are certain intrinsic and environmental features of a species that push it towards a scavenging lifestyle. These can be thought of as some of the principal parameters in optimal foraging theory namely, encounter rate, handling time and prey availability. We use these components to highlight the morphologies and environments that would have been conducive to scavenging over geological time by focusing on the dominant vertebrate groups of the land, sea and air. The result is a document on the natural history of scavenging, the first to our knowledge. Our idea of a scale of scavenging can be applied to any species at any time to judge the importance of this behaviour in its diet.

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 (DeVault et al. 2003). Professor Sanborn Tenney writing in 1877 for The American Naturalist 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 (Tenney 1877). 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 does not only feed on animals too big for it to have hunted. The obvious lack of direct behavioural data compounds the difficulty of discerning scavenging from predation among extinct forms. Indeed, a single species of dinosaur notwithstanding (Carbone et al. 2011), a synthesis describing the natural history of scavengers is absent from the literature. With research on scavenging on the rise (Koenig 2006) 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" (Beasley et al. 2015). This has profound implications for the trophic ecology of these systems and particularly our models of them. Even Tenney’s noble big cats are now known to take in a significant portion of carrion in their diet where some lion populations acquire over 50% of their meat from carcasses (Jones et al. 2015). While recognising the difficulty in directly observing scavenging, it is possible to turn to other methods in order to discern the most suitable morphologies, physiologies and environments for a scavenging lifestyle to prosper. Here we chart the natural history of scavenging by assessing the potential for the behaviour in dominant vertebrate

groups given their ecology and functional traits.

The Challenges of Scavenging

The chief hurdle to scavenging is finding a resource that is often difficult to predict in space and time. Through chance alone many species will avail of some opportunistic scavenging. However, species that rely on scavenging to sustain substantial portions of their diets must encounter a sufficient amount of carrion in order to meet their energetic demands. Once found, the scavenger must be able to out-compete any potential competitors and process the, typically decaying, carcass replete with micro-organism derived toxins (Ruxton et al. 2014). These characteristics can be assumed to be under evolutionary selection pressures for traits that increase carrion discovery and monopoly. Finally, the potential for scavenging will also depend on the density, size, and quality of carcases produced, all of which are affected by complex ecosystem dynamics but are outside the selection pressures on the scavenger. Each of these facets are essentially the backbone of fundamental ecological theory and are the key parameters defined in functional response curves, namely encounter rate, handling time and prey availability (Jeschke et al. 2002). By considering scavenging in this context of optimal foraging we can identify the prerequisite attributes and processes required for the behaviour. This has enabled us to propose a scale of scavenging whereupon we can place any vertebrate species, past or present, and assess the likely importance of carrion in its diet.

Encounter Rate

All foraging processes depend on the encounter rate between consumer and resource. Locomotory speed, foraging time and detection radius all increase the encounter rate between a scavenger and the carcasses it is searching for. Alternatively, a species can reduce its metabolic requirements so that it can survive long periods between meals. We would thus

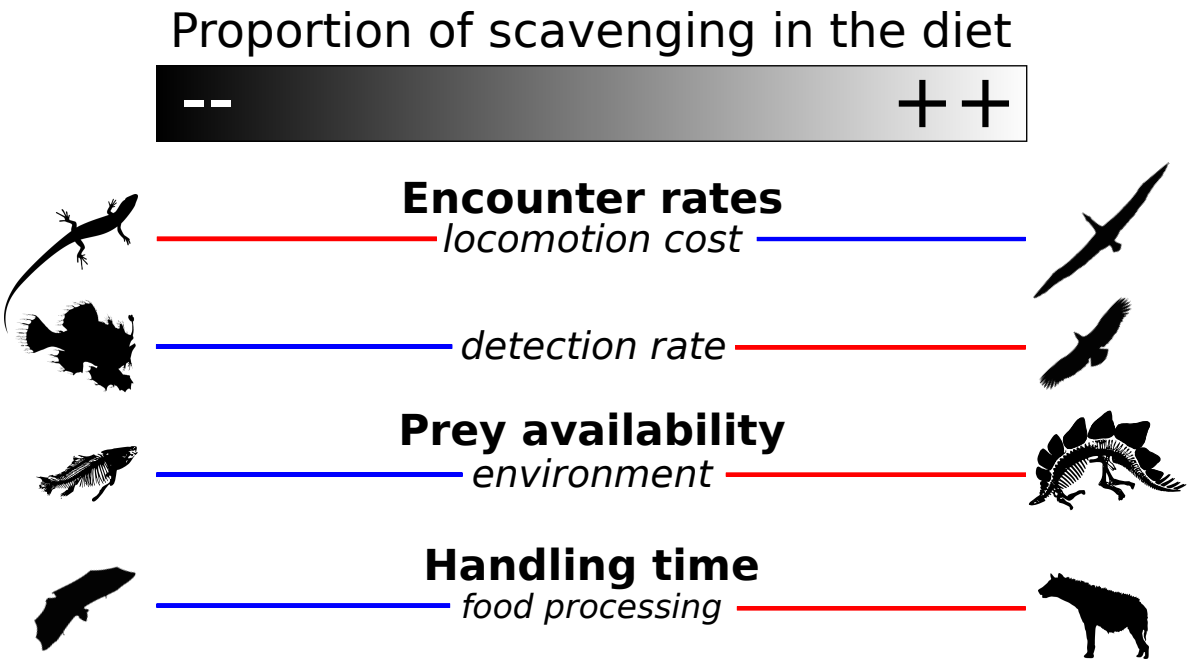

Figure 1: Factors influencing the proportion of scavenging in a vertebrates' diet. Blue lines indicate a reduction in the factor and red lines indicate an increase.

expect selection pressures to act on the various traits that govern these parameters.

However, as we noted above, encounter rate is also determined by the productivity of the environment, something which the selective forces acting on the scavenging have no control over.

Metabolism

Because of the sporadic nature of carrion we would expect adaptations that reduce energetic costs of maintenance to be selected for in scavengers as it would allow for longer inter-feeding periods. Extant reptiles possess an advantage here, in that over the course of a year their food requirements can be 30 times lower than an endotherm of equal size (Nagy 2005). 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). The same reasoning can be applied to crocodiles and their allies (Forrest 2003) because a sit and wait strategy is viable for an ectotherm (Forrest 2003, Moleón et al. 2015). Carey et al. (1982) found ectothermic sharks have the ability to exist weeks between meals because they focus on the energy-rich sections of carcasses (see Handling Time). Endotherms have also evolved physiological mechanisms that allow them to depress their otherwise high metabolic rates at certain times e.g. vultures who do so while resting at their roost and during periods of food deprivation (Bahat et al. 1998).

Locomotion

Because of the inherent unpredictability of carrion, scavenging depends more on the ability to efficiently move over large areas than does predation. This generally requires an efficient transfer of metabolic energy into movement which relies on the animal's anatomy and physiology as well as the medium of the environment in which the animal is moving (i.e. aerial, aquatic or terrestrial). Perhaps the most efficient form of locomotion in vertebrates is, paradoxically, found in flying species. Despite the energetic costs of flight, the only known vertebrate obligate scavengers are the old and the new world vultures. While powered flight is energetically expensive, species like vultures have evolved behavioural and anatomical features to exploit air currents using their large wingspans, allowing them to soar at a cost of only twice their metabolic rate (Hedenstrom 1993, Spivey et al. 2014). By depending on thermal air flows these species can forage over vast ranges (Spiegel et al. 2013). An analogous mode of locomotion is also exploited by seabirds, who use strong ocean winds to search large areas of the oceans (Norberg 2012, Thaxter et al. 2012). While many species of seabird are likely primarily predators, it seems that albatrosses, who can range many hundreds of kilometres, take a substantial amount of carrion in their diet (Croxall and Prince 1994). This is typically in the form of squid carcases, which float on the surface, allowing the birds to readily pluck their remains out of the water (Croxall and Prince 1994).

The groups from which these modern soaring birds arose, appear during the Palaeocene (66 - 56 Million years ago (Mya); Jetz et al. 2012, Jarvis et al. 2014) and Cretaceous (Chiappe and Dyke 2006) respectively. However, soaring flight is likely to be far older than this with avian flight originating in the Late Jurassic (163.5-145 Mya) and vertebrate flight in the Late Triassic (235-201.3 Mya) coincident with the pterosaurs. Indeed, scavenging among pterosaurs has been hypothesised many times before (Witton and Naish 2008). Certain groups of these animals could reach enormous sizes (e.g. Azhdarchids with wingspans of 11 metres; Witton and Habib 2010) and, notably, appear to have engaged in soaring flight

(Witton and Habib 2010). It seems probable that at least some of these extinct species used soaring as a means for scavenging (Witton 2013). While soaring is perhaps the only viable means of locomotion that allows for an obligate, scavenging life-style (Ruxton and Houston 2004b), powered flight is still an efficient means of locomotion. Certainly, avian flight is cheaper than either walking or running (Tucker 1975).

We know that many extant birds exist as facultative scavengers because storks, raptors and corvids all take substantial quantities of carrion in their diet (Kendall 2013). Similarly we would expect that extinct species would also scavenge in a similar fashion depending on the efficiency of their flight. For example, early birds such as *Archaeopteryx* are predicted to have been poor, relatively inefficient fliers (Nudds and Dyke 2010) and so ill-suited to finding carrion. The importance of efficient flying over large areas may explain the lack of scavenging behaviour in bats as they are generally nocturnal, a time when they would receive no aid from convective air currents (Norberg 2012).

Similar to aerial species, aquatic scavengers have a locomotory benefit because water is a medium that is conducive to low-cost movement (Tucker 1975, Williams 1999). This has led some researchers to argue for the likelihood of an obligate scavenging fish (Ruxton and Houston 2004a, Ruxton and Bailey 2005).

Sharks are one likely candidate for general scavenging behaviors as their locomotion, which depends on large pectoral fins to generate lift as they swim, resembles that of the large soaring fliers. Many shark species have large foraging ranges (e.g. the great white sharks *Carcharodon carcharias*; Bruce et al. 2006) and it seems reasonable that they would use oceanographic currents to further reduce movement costs (Ruxton and Houston 2004a). In fact, facultative scavenging is seen in many selachian groups, including species of extant sharks like white sharks (known to feed on whale carcasses; Fallows et al. 2013), Greenland sharks (feeding on seals; Watanabe et al. 2012), and sixgill sharks (Anderson and Bell 2016). There is evidence too of scavenging in extinct species, where shark teeth have been found in

the remains of dinosaurs, mosasaurs and Pliocene mysticete whales (5.3-3.6 Mya; Schwimmer et al. 1997, Ehret et al. 2009).

Interestingly, style of swimming in fish does not significantly affect the cost of movement (Williams 1999), hence it is likely that many aquatic species with large ranges will encounter scavenging opportunities. It is perhaps jaw morphology that is more likely to define which species can avail of carcasses.

We might expect then that by combining an aquatic environment and an endothermic metabolism marine mammals would especially prosper as scavengers. Fossil pinnipeds and cetaceans from 60 Mya have transitional features indicative of their evolutionary trajectory to fully aquatic species (Williams 1999). But despite their movement away from land their energetic savings were negligible because the *total* cost incurred by a swimming marine mammal is high (Williams 1999). Indeed, the total energetic cost is similar to an equivalent terrestrial or aerial mammal (Williams 1999). This underscores the trade offs between the benefits of endothermy in terms of activity periods and the costs of maintaining such an energetically expensive system. That said, aquatic endotherms have and do scavenge. For instance, early whales such as *Basilosaurus* (38-36.5 Mya) seem to have fit into the same niche as killer whales (*Orcinus orca*) and we have some evidence for scavenging in both (Fahlke 2012, Whitehead and Reeves 2005).

Terrestrial environments are the most energetically costly in which to move (Tucker 1975). Unlike aerial and aquatic environments support must be provided through the animal's posture. The early transition from a sprawling gait, seen in early tetrapods, to the more erect posture of synapsids and later dinosaurs and mammals, has often been supposed as conferring a huge advantage to the latter groups (Sullivan 2015). The purported advantages include benefits in terms of speed, efficiency, muscle effort and manoeuvrability (Sullivan 2015). Clearly, for a scavenger, an ability to efficiently cover an area at a high speed would increase the encounter rate with carrion. Despite being intuitive, Sullivan (2015) states most

of the hypotheses in favour of this idea remain to be tested in the context of archosaur evolution. One noted consequence of a sprawling gait is the phenomenon known as Carrier's constraint such that the animal can't move and undergo costal ventilation at the same time because the lateral movements impedes its lungs (Carrier 1987). The evolution of an upright posture has been offered as one of the primary mechanisms that allowed early archosaurs to overcome this constraint (Uriona and Farmer 2008).

Whatever the case, it is with the evolution of endothermy in the therapsid-mammal lineage (Clarke and Pörtner 2010) that terrestrial vertebrates would have gained the ability to range more widely, a vital component in seeking out carrion. Modern endothermic mammals can sustain longer periods of energetically expensive activity (Bennett and Ruben 1979) resulting in larger foraging ranges. Today, terrestrial scavenging in the mammals is probably best known in an African context where hyenas, jackals and lions all take sizeable proportions of carrion in their diet. In the spotted hyena (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*) and brown hyena (*Hyaena brunnea*) it can be over 90% (Jones et al. 2015). And although no contemporary terrestrial vertebrate exists as an obligate scavenger, most, if not all, are facultative to some extent (Beasley et al. 2015). The particular reliance of hyenas on carrion means we can use them as examples of efficient terrestrial scavengers to compare with other forms. In terms of locomotion, they employ a characteristic "rocking horse gait" which allows them to cover great distances efficiently, loping at 10 km/hr (Mills 1989, Jones et al. 2015). Such long-distance travel is apparent in African wild dogs (*Lycaon pictus*) and many other canids (Pennycuick 1995, Janis and Figueirido 2014). In contrast, big cats like leopards (*Panthera pardus*) rely on ambush (Pennycuick 1995). This allows us to make a broad distinction between the ambush strategies of cat-like forms and the pursuit/ pounce strategies of more dog-like forms, the latter being more suited to scavenging (Janis and Figueirido 2014). These insights allow us to compare extant terrestrial species to their prehistoric forebears given the dominance of mammalian carnviores since the Eocene (56-33.9

Mya) where the order split into the Caniforma and Feliforma (Van Valkenburgh 1987). To take one example, Anyonge (1996) found that *Nimravides*, a genus of sabretooth cat from the Miocence (10.3 to 5.3 Mya), were likely to have been ambush predators which would argue against them taking a lot of carrion.

Of course, terrestrial animals can also move bipedally. Although the evolution of bipedal movement was significant in that it freed up the forelimbs for other purposes (e.g. climbing, tool-use, wing development etc.) it does not differ radically in cost from quadrupedal locomotion (Williams (1999), and references therein). For instance, Alexander (2004) shows that, in the case of humans, we are more economical than predicted while walking and less so while running according to predicted costs of terrestrial movement. Our locomotory efficiency has fed into the question of where our ancestors placed on the hunter-scavenger axis during the Plio-Pleistocene, which has been a matter of debate for years (Domínguez-Rodrigo 2002). Ruxton and Wilkinson (2013) added to this debate with his argument that long distance endurance running, often used by humans for hunting, was not an important feature of hominin scavenging. They arrive at this conclusion on the basis of the high cost of running coupled with the fact that dangerous competitors will tend to arrive beforehand.

Aside from humans and our allies, the best-known terrestrial bipeds are the dinosaurs and unsurprisingly, given their enduring appeal, the prevalence of scavenging has been extensively explored in the carnivorous theropods. These were the dominant terrestrial carnivores for most of the Mesozoic Era (252.17 - 66 Mya) and ranged from the chicken-sized to the whale-sized, all of which were bipedal. While the locomotory ability of theropods has been debated since their first inception, more recent studies have reconstructed them as relatively mobile animals (Pontzer et al. 2009). Despite some suggestions that larger species may have had some advantage in scavenging, partially due to the ability to search large areas (Ruxton and Houston 2003), more recent studies have shown that the energetic demands of such large forms meant scavenging was likely more prevalent in mid-sized theropods of

approximately half a tonne (Carbone et al. 2011, Kane et al. 2016).

Detection

As predicted by the importance of an increased encounter rate, known scavengers have evolved well-developed senses, with the visual and olfactory sensory systems most often associated with scavenging behavior. This is perhaps no surprise because sensory systems that rely on detecting signals associated with living animals, such as audioception, electroreception, thermoreception and echolocation will be limited in their ability to detect an already dead animal.

Apart from the basic capacity of these senses to detect carrion, how they function in different environments is also important. In the simplest case, the search space is a two dimensional plane (Pawar et al. 2012). If the scavenger itself is searching on the plane, as is so for terrestrial species, the detection range is simply defined by the radius of their sensory organs. Consequently, the ability to detect carrion can be seriously restricted for visually reliant, terrestrial species. They may overcome this restriction however, by using olfaction, which is less affected by the relief of the land. For example, hyenas have the ability to smell a rotting carcass 4 km away (Mills 1989), which exceeds the 500 m range deemed necessary by Ruxton and Houston (2004b) to be able to survive as a scavenger.

Indeed, the olfactory senses of many extant (and in all probability extinct) carnivores meet this required distance, making scavenging feasible for most terrestrial carnivores (Farlow 1994, Mech and Boitani 2010). Among extinct species in particular, we can use the ratio of olfactory bulb to brain size to infer a preference for olfactory foraging (Zelenitsky et al. 2011). This approach was used by Zelenitsky et al. (2011) to hypothesise such a mode for the theropod dinosaur *Bambiraptor* and by Witmer and Ridgely (2009) for tyrannosaurs. The flying pterosaurs however, had tiny olfactory bulbs indicating this sense was not relied on (Witton 2013).

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. Certainly, 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). Eagles too are known to have highly developed vision (Reymond 1985). The flying pterosaurs also convergently evolved large orbits and optic lobes (Witton 2013). It follows that the evolution of flight allowed aerial animals to detect far more carrion than their terrestrial counterparts through vision (Lisney et al. 2013).

Existing in this '3D' environment also means being able to gather a wealth of information from other foragers, be they conspecifics or otherwise (Jackson et al. 2008). Again, returning to vultures, the genus *Gyps* consists of highly social and colonially nesting species (Fernández-Bellon et al. 2015). These behaviours allow them to forage far more efficiently because one bird can scrounge information on the location of food from another successful forager (Kane et al. 2014). Information transfer of this kind is typically inadvertent and as a consequence no complex social interactions are required, simply the ability to recognise a successful forager. Thus, it seems probable that scrounging behaviours were seen in the flying pterosaurs as well.

The terrestrial-olfaction, aerial-visual divide is not total though. Terrestrial species like hyenas and hominins exploit the efficiency of birds by looking to the skies for groups of vultures to follow to carrion (Jones et al. 2015, Ruxton and Wilkinson 2013). And many birds, e.g. turkey vultures (*Cathartes aura*), have well-developed olfactory systems (Lisney et al. 2013) which they use to forage in heavily forested areas where vision is limited (Houston 1986).

Although aquatic species also have a vertical component to their environment, they must

contend with low-light levels where visual detection distances are far lower ($<$ 100 m) than they would be for air. As such, aquatic animals detect resources through chemo- and mechanoreception more so than through vision (Ruxton and Houston 2004a). This is particularly relevant to sharks and aquatic snakes who are deemed as having the most suitable physiology 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 by snakes. This gained some support from DeVault and Krochmal (2002), who found a preponderance of aquatic snake species in their review of this behaviour. Smell seems to be the primary means of carcass detection in sharks as well. Fallows et al. (2013) found that wind speed determined the number of sharks feeding at whale carcasses, indicating they were dependent on detecting the odours from the decaying whales.

Prey Availability

The environmental influence on prey availability is an aspect that greatly affects encounter rate but is invisible to the selective forces acting on the scavenger. Aspects including, primary productivity, relief, and temperature will all greatly affect scavenging tendency. Ruxton and Houston (2004b) suggest an historic ecosystem with a productivity similar to the Serengeti could have supported an *obligate* mammalian or reptilian terrestrial scavenger. Indeed, in systems that were dominated by large ectothermic or mesothermic herbivore vertebrates, the same primary productivity would have supported a greater biomass, due to the scaling of mass with metabolic rate (McNab 2009). The upshot of this may have been a higher biomass of herbivores dying and offering scavenging opportunities (although these larger species may have also lived longer).

In fact, scavenging behaviour may have evolved on land as soon as the first terrestrial tetrapods emerged. Some of the earlier tetrapods tracks dating back to the early Middle Devonian (393.3 - 387.7 Mya) were found in intertidal environments (Niedzwiedzki et al.

2010). These environments are isolated from marine systems twice a day leaving potential carrion unexploited by marine vertebrates. Niedzwiedzki et al. (2010) suggest that these environments "would thus have allowed marine ancestors of tetrapods gradually to acquire terrestrial competence while accessing a new and essentially untouched resource."

Staying in the aquatic setting, the phenomenon of occasional bounties of carrion in the form of whale falls has led some researchers to investigate if an obligate 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 find 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 cetaceans, including *Leedsichthys*, a bony fish from the Middle Jurassic (174.1-163.5 Mya) and the aquatic Mesozoic reptiles, the plesiosaurs, pliosaurs and ichtyosaurs, that could all exceed 15 metres in length (Ruxton 2011, Danise et al. 2014).

So, despite being unlikely, the energetic feasibility of a marine scavenger that specialises on large carcasses has a long history. One point of interest is that of the whaling industry, which provided a bonanza of floating carcasses especially during the 20th century (Whitehead and Reeves 2005). This meant killer whales could switch from hunting to scavenging, a switch made that much easier by the noise of the whaling vessels that would effectively ring the "dinner-bells" (Whitehead and Reeves 2005).

Perhaps the greatest environmental driver of scavenging tendency is that of temperature. The geological record shows the Earth has undergone radical fluctuations in temperature over time. This will have had a significant bearing on the availability and persistence of carrion. To illustrate the point, a 10°C increase in ambient temperature can double carcass decomposition rates (Parmenter and MacMahon 2009) and geological evidence indicates that the Mesozoic Earth was on average at least 6 °C warmer than now (Sellwood and Valdes

2006). In terms of specific habitats, it has been shown that decomposition is greater in warm and moist areas versus more xeric ones (Beasley et al. 2015). Moreover, oceanic productivity and habitat structure are all impacted by climactic conditions. The impacts these can have on scavengers have been empirically supported e.g. Beasley et al. (2015) who point to a series of studies showing how microbes and invertebrates benefit at higher temperatures to the detriment of vertebrate scavengers such that "above 20°C vertebrates were able to detect and consume only 19% of small-mammal carcasses, whereas at temperatures below 18°C, vertebrates consumed 49% of carcasses". This is a sobering thought given the impact we humans are having on the Earth's climate.

Handling Time

Since the food a scavenger depends upon is not dispatched directly, often the most easily accessible and choicest components of the carcass will be missing or, if present, will be subject to decay as well as competition. So being able to overcome competitors and maximise the nutrient gain from the remnants are all essential parts of carcass handling time.

Competition

Large body size has substantial advantages in agonistic interactions (Ruxton and Houston 2004b). For instance, lions can acquire much of their carrion through kleptoparasitism of hyena kills (Trinkel and Kastberger 2005). This line of reasoning suggests that some theropod dinosaurs, who could get up to 15 tonnes, would have had easily monopolised a carcass (Weishampel et al. 2004) provided they could find them efficiently (Kane et al. 2016).

We would expect this trait to be selected for even in the case of weight-constrained, scavenging fliers. This is true for wandering albatrosses (*Diomedea exulans*), cinereous vultures (*Aegypius monachus*) and condors (*Vultur gryphus*, *Gymnogyps californianus*) who

all have body masses that can exceed 10 kg and represent some of the heaviest bird species capable of flight (Weimerskirch 1992, Ferguson-Lees and Christie 2001, Donázar et al. 2002). Indeed, such is the competitive advantage held by vultures over other facultative scavenging birds that temporal niche partitioning at the carcass has evolved (Kendall 2013, Kane et al. 2014). Additionally, many pterosaurs were far bigger again, with estimated body masses of over 200 kg in the Azhdarchids (Witton and Habib 2010). Although Witton and Naish (2008) argued that neck inflexibility and straight, rather than hooked jaw morphology points against Azhdarchids existing as *obligate* scavengers, their terrestrial proficiency indicates they would have been comfortable foraging on the ground. Extant Marabou Storks (*Leptoptilos crumenifer*) have a comparable morphology and are noted facultative scavengers (Monadjem et al. 2012) so it is reasonable to believe that these pterosaurs behaved similarly.

By contrast, extant bats seem poorly equipped to deal with competitors. Their poor terrestrial ability, smalls size and cost of movement on the ground would count against them while attempting to fend off other species at a carcass (Riskin et al. 2006, Voigt et al. 2012).

Smaller species can compensate for a lack of individual body size by weight of numbers in competitive interactions. This is true for a host of notable scavengers, such as vultures, early hominins and hyenas, who can dominate larger competitors provided they substantially outnumber them (Kane et al. 2014, Trinkel and Kastberger 2005, Ruxton and Wilkinson 2013).

Direct confrontation can be circumvented by certain behavioural adaptations. The evolution of nocturnal behaviour in some mammals, for instance, has been put forth as an adaptation to reduce competition with the exclusively diurnal vultures (Gittleman 2013). In areas absent of vultures such as the Arctic, terrestrial carnivores like bears and wolves take more carrion (DeVault et al. 2003) Thus, in the Palaeozoic, the absence of flying vertebrate competitors may have permitted terrestrial forms to take in a higher proportion of carrion in their diet.

In addition to fending off other vertebrates, scavengers also have to contend with competition from micro-organisms, which requires a specialised physiology. Although the findings of Shivik (2006) that "evolutionary pressures favor detection maximizers relative to toxification minimizers in competitive interactions for carcasses." appear sound, the fact remains that overcoming micro-organism toxins is still a beneficial adaptation to any scavenger. Avian scavengers have evolved incredibly acidic stomachs that allow them to consume and process putrefied flesh with no ill effects (Houston and Cooper 1975, Roggenbuck et al. 2014). This adaptation is not restricted to vultures though, Grémillet et al. (2012) showed wandering albatrosses (*Diomedea exulans*; so-called "vultures of the seas") had an average pH of 1.5, which enables them to consume fisheries discards and squid carcasses. There is also evidence of selection for "toxification minimizers" beyond birds among the ectotherms. From our earlier arguments we know that ecthotherms are limited in their ability to find carrion as quickly as endotherms. These later arrivers would thus benefit especially from well-developed detoxifying apparatus. Shivik (2006) suggests that "specialized oral structures in snakes may have evolved under pressures associated with scavenging." Moreover, some researchers have charted an evolutionary course from basal fossorial snakes to modern terrestrial species by way of an obligate scavenger intermediate (Bauchot 2006).

Food Processing

Aside from coping with competitors, another vital component of carrion handling time is the ability to maximise the energy gain from the remains. At whale carcases, white and blue sharks are known to preferentially feed on the blubber layer (Long and Jones 1996). Blubber is an energy rich portion of the carcass that can allow a shark to survive for 1.5 months on 30 kg of the material (Carey et al. 1982). On land many scavengers utilize late-stage carcass material that is less subject to decomposition and may be unavailable to other competitors, for example bone. Osteophagy is known across a range of terrestrial carnivores and given that

some fat-rich mammalian bones have an energy density (6.7 kJ/g) comparable with that of muscle tissue, it makes skeletal remains an enticing resource (Brown 1989). This ability reached its zenith among hyenas with the evolution of the estimated 110 kg *Pachycrocuta brevirostris* during the Pliocene (3.6 - 2.58 Mya; Palmqvist et al. 2011). Indeed, their extinction has been blamed on the decline of sabretooth cats (Machairodontinae), the unique skull morphology of the latter meant they would leave a large amount of food on a carcass for would-be scavengers (Palmqvist et al. 2011). Earlier in the evolution of mammals, the bone-crushing dogs that evolved during the Oligocene (Borophaginae; 33.9 - 23.03 Mya) have also been compared to hyenas in terms of their feeding ecology (Van Valkenburgh et al. 2003, Martín-Serra et al. 2016).

In Mesozoic systems some large theropod dinosaurs had a morphology indicative of an ability to process bone (e.g. the robust skull and dentition of *Tyrannosaurus rex;* Hone and Rauhut 2010). 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) which would have been powerful enough to break open skeletons (Rayfield et al. 2001). Osteophagy may have been even more viable during the Mesozoic era as well because of this skewed body mass distribution of herbivores 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).

Despite not having the anatomical ability to break open bone, the bearded vulture (*Gypaetus barbatus*) has evolved a technique whereby it drops long bones from a height, splintering them on the rocks below which allows them to feed (Margalida 2008). Similarly, early hominins developed the ability to craft tools for breaking open bones (Blasco et al.

2014). A recent study investigating potential scavenging opportunities for hominins in Kenya found that, in addition to skeletal material, there is a substantial amount of scavengeable meat left on predated remains; sufficient to sustain the requirements of an adult male *Homo erectus* (Pobiner 2015). In some historical hominin-inhabited areas there were a greater number of felids than hyenids. Again, this is significant because hyenas are likely to have left far less flesh on a carcass than a felid such as a sabretooth, enabling contemporaneous hominins to benefit (Pobiner 2015). The use of tools and the cooperative nature of hominins meant they could likely get a substantial part of their energetic requirements through scavenging depending on their environment (Moleón et al. 2014).

On the ground, and despite the advantages of social resource defence, the competitive ability of even the largest flying bird is radically diminished in their interactions with mammalian competitors, and as such they tend to consume carrion rapidly. Houston (1974) observed a group of *Gyps* vultures consuming all of the soft tissue from a 50 kg Grant's gazelle (*Nanger granti*) in eight minutes. Their serrated tongues and hooked bills enabling them to achieve this feat (Houston and Cooper 1975). Aside from raptors, the specialised beaks of many modern bird lineages tends to hinder their ability to eat meat which is in contrast to the first lineages that did not have this feature (Martyniuk 2012). As Martyniuk (2012) notes these early birds would thus have been predominantly carnivorous, implying scavenging was a live opportunity cf. their descendants. Among the pterosaurs, Witton (2013) makes the case that the istiodactyl pterosaurs were the most likely scavengers of this group based on their potential handling time. The mix of strong and weak features in their skull morphology is indicative of animals that were suited to removing large amounts of flesh from an immobile foodstuff (Witton 2013).

Again, we can draw a comparison with clades that are lacking in these features. As we mentioned earlier the skull morphology of extinct sabretooths meant they would have left a large amount of flesh on a carcass and were unable to feed on bones (Palmqvist et al. 2011).

Extant bats are also poorly equipped when it comes to feeding on carrion; the larger forms are typically frugivores and therefore lack the adaptations for digesting meat, while the smaller carnivorous bats are mainly found in the microbats, which are insectivorous (Aguirre et al. 2003). That said, Necromantis ("death-eater"), a large bat from the middle to late Eocene (56-33.9 Mya) had a robust cranio-mandibular morphology, and is a likely candidate for an extinct scavenging bat (Weithofer 1887, Hand et al. 2012).

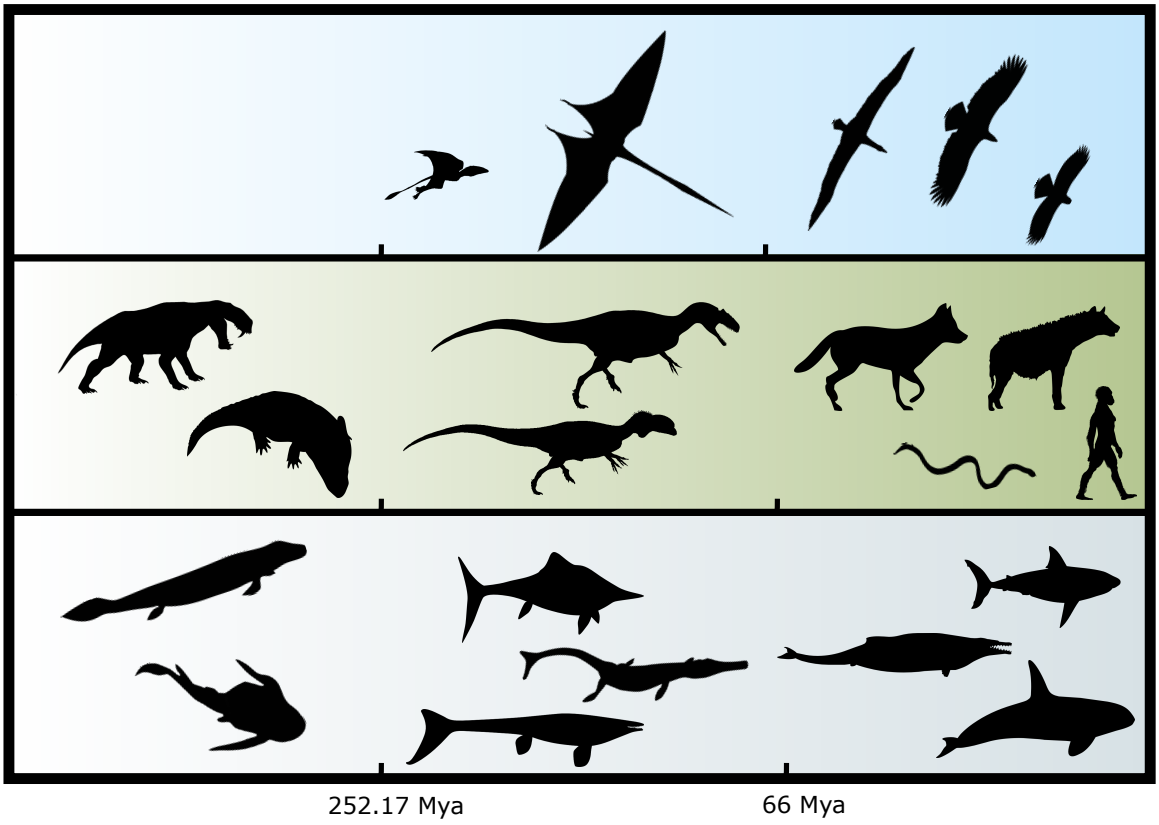

Figure 2: The diversity of scavengers through time. Each species has either direct evidence for it being a scavenger or would be positioned high up on our scavenging scale.

Conclusion

As is often the case in science, the present provides the key to the past. The animals of today, while often different (sometimes radically so) to their ancestors, can be used to make informed comparisons to extinct species. We have used this technique to give insight into the drivers of scavenging across vertebrates through time. In common with any other forager be they grazer, browser or predator, scavengers past and present have had to balance their energetic costs with the gains of food. The main factors we considered namely, encounter rate, handling time and prey availability can be used to create a scale of scavenging whereupon any species can be placed in order to establish the importance of carrion in it diet. We hope this approach will be useful in the effort to explore this most understudied of feeding ecologies.

Appendix

Scaling relationships for sustainable travel speed are 1.15 $\times$ body mass (kg) $^{0.12}$ and 0.23 $\times$ body mass (kg) $^{0.12}$ for mammals and reptiles respectively (Ruxton and Houston 2004b). These are fed into the foraging model $\frac{\mathsf{duration} \times \mathsf{speed}}{2}/1000$ (Enstipp et al. 2006).

Acknowledgments

A lot of people are to thank here.

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