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4 **A Recipe for Scavenging - the natural history of a**  
5 **behaviour**

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## 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.

# 1 Introduction

2 Historically, scavengers have not been viewed as the most charismatic of animals. This may  
3 go some way to explaining the gap in our knowledge of the prevalence of this behaviour  
4 (DeVault et al. 2003). Professor Sanborn Tenney writing in 1877 for *The American Naturalist*  
5 had this to say about one well known group, "prominent among the mammalian scavengers  
6 are the hyenas, the ugliest in their general appearance of all the flesh eaters." He contrasts  
7 these with "nobler kinds" of carnivores such as lions and tigers (Tenney 1877). Even aside  
8 from our own subjective biases, scavenging is a difficult behaviour to detect after the fact.  
9 Without catching a carnivore in the act of killing we are left to infer how the prey was killed.  
10 Some simple heuristics can inform us, for instance, in cases where the prey item was simply  
11 too large to have been killed by the ostensible predator (Pobiner 2008). But clearly, a  
12 scavenger does not only feed on animals too big for it to have hunted. The obvious lack of  
13 direct behavioural data compounds the difficulty of discerning scavenging from predation  
14 among extinct forms. Indeed, a single species of dinosaur notwithstanding (Carbone et al.  
15 2011), a synthesis describing the natural history of scavengers is absent from the literature.  
16 With research on scavenging on the rise (Koenig 2006) we are now beginning to realise the  
17 extent of this behaviour such that, "in some ecosystems, vertebrates have been documented  
18 to assimilate as much as 90% of the available carrion" (Beasley et al. 2015). This has  
19 profound implications for the trophic ecology of these systems and particularly our models of  
20 them. Even Tenney's noble big cats are now known to take in a significant portion of carrion  
21 in their diet where some lion populations acquire over 50% of their meat from carcasses  
22 (Jones et al. 2015). While recognising the difficulty in directly observing scavenging, it is  
23 possible to turn to other methods in order to discern the most suitable morphologies,  
24 physiologies and environments for a scavenging lifestyle to prosper. Here we chart the natural  
25 history of scavenging by assessing the potential for the behaviour in dominant vertebrate

1 groups given their ecology and functional traits.

## 2 **The Challenges of Scavenging**

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

## 19 **Encounter Rate**

20 All foraging processes depend on the encounter rate between consumer and resource.  
21 Locomotory speed, foraging time and detection radius all increase the encounter rate between  
22 a scavenger and the carcasses its searching for. We would thus expect selection pressures to  
23 act on the various traits that govern these parameters.

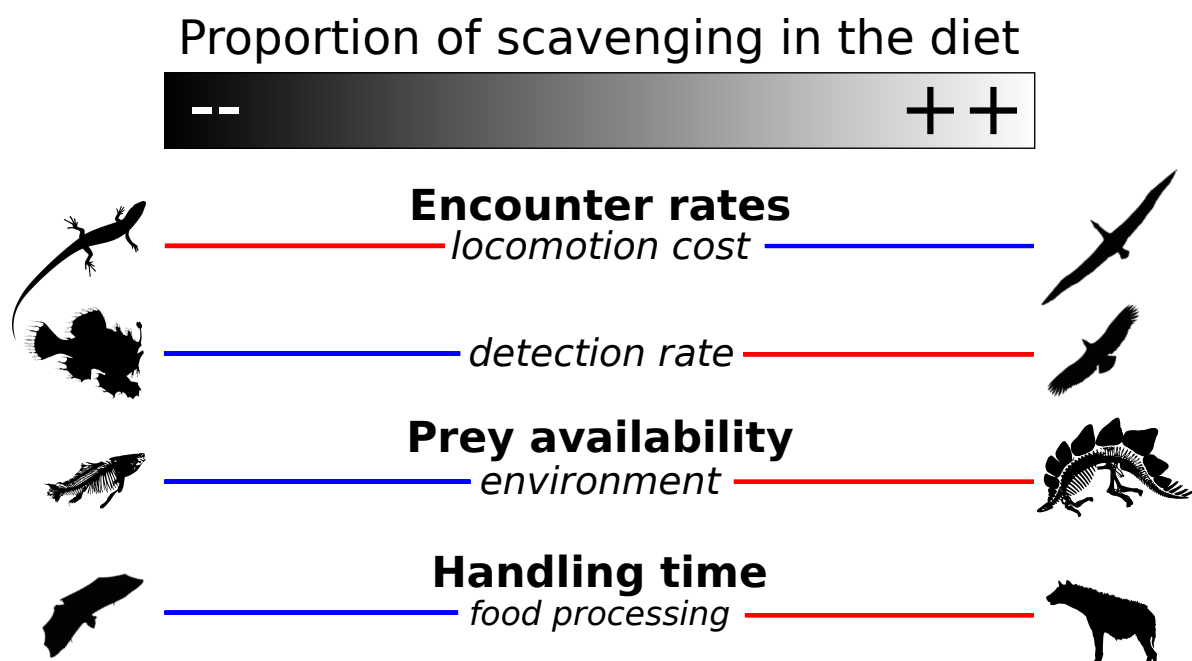


Figure 1: Factors influencing the proportion of scavenging in a vertebrates' diet. Blue lines indicate a reduction in the factor and red lines indicate an increase.

## 1 Locomotion

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

19 The groups from which these modern soaring birds arose, appear during the Palaeocene  
20 (66 - 56 Million years ago (Mya); Jetz et al. 2012, Jarvis et al. 2014) and Cretaceous  
21 (Chiappe and Dyke 2006) respectively. However, soaring flight is likely to be far older than  
22 this with avian flight originating in the Late Jurassic (163.5-145 Mya) and vertebrate flight in  
23 the Late Triassic (235-201.3 Mya) coincident with the pterosaurs. Indeed, scavenging among  
24 pterosaurs has been hypothesised many times before (Witton and Naish 2008). Certain  
25 groups of these animals could reach enormous sizes (e.g. Azhdarchids with wingspans of 11  
26 metres; Witton and Habib 2010) and, notably, appear to have engaged in soaring flight

1 (Witton and Habib 2010). It seems probable that as least some of these extinct species used  
2 soaring as a means for scavenging (Witton 2013). While soaring is perhaps the only viable  
3 means of locomotion that allows for an obligate, scavenging life-style (Ruxton and Houston  
4 2004b), powered flight is still an efficient means of locomotion. Certainly, avian flight is  
5 cheaper than either walking or running (Tucker 1975).

6 We know that many extant birds exist as facultative scavengers because storks, raptors  
7 and corvids all take substantial quantities of carrion in their diet (Kendall 2013). Similarly we  
8 would expect that extinct species would also scavenge in a similar fashion depending on the  
9 efficiency of their flight. For example, early birds such as *Archaeopteryx* are predicted to have  
10 been poor, relatively inefficient fliers (Nudds and Dyke 2010) and so ill-suited to finding  
11 carrion.

12 The importance of efficient flying over large areas may explain the lack of scavenging  
13 behaviour in bats as they are generally nocturnal, a time when they would receive no aid from  
14 convective air currents (Norberg 2012).

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

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

1 There is evidence too of scavenging in extinct species, where shark teeth have been found in  
2 the remains of dinosaurs, mosasaurs and Pliocene mysticete whales (5.3-3.6 Mya;  
3 Schwimmer et al. 1997, Ehret et al. 2009).

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

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

20 Terrestrial environments are the most energetically costly in which to move (Tucker  
21 1975). Unlike aerial and aquatic environments support must be provided through the animals  
22 posture leading to trade offs between low cost of maintain and the efficiency of transport.  
23 For example, the sprawling posture of many ectotherm groups (except frogs!) would be  
24 expected to allow for a lower maintenance cost relating to body support in comparison to  
25 groups with the limbs position underneath the body, such as mammals, aves and dinosaurs.

26 While the low maintenance costs of a sprawling like posture may reduce the need to



1 scavenge frequently, the ability to search large areas is several restricted in these groups  
2 hence likely reducing such opportunities (ref on home range of terrestrial ectotherms). For  
3 example, a sprawling gait can results in the phenomenon known as Carrier's constraint such  
4 that the animal can't move and breathe at the same time because the lateral movements  
5 impedes its lungs (Carrier 1987). On the other hand the more erect body positions and often  
6 associated higher basal metabolic rates, allow for sustained locomotion over long periods of  
7 time and hence allow such species to search large areas.

8 The early transition from a sprawling gait, such as seen in *Tiktaalik*, to the more erect  
9 posture of Synapsids and later dinosaurs and mammals, has often been supposed as  
10 conferring a huge advantage to the latter. Despite being intuitive, Sullivan (2015) states  
11 most of the hypotheses in favour of this idea remain to be tested in the context of archosaur  
12 evolution.

13 Whatever the case, it is with the evolution of endothermy in the therapsid-mammal  
14 lineage (Clarke and Pörtner 2010) that terrestrial vertebrates would have gained the ability to  
15 range more widely, a vital component in seeking out carrion. Although the earliest evidence  
16 of vertebrate scavenging comes from the Permian (298.9 - 252.17 Mya) where a  
17 temnospondyl amphibian fed on the carcass of *Varanops*, a predatory synapsid of the time  
18 (Reisz and Tsuji 2006).

19 Modern endothermic mammals can sustain longer periods of energetically expensive  
20 activity (Bennett and Ruben 1979) resulting in larger foraging ranges. Today, terrestrial  
21 scavenging in the mammals is probably best known in an African context where hyenas,  
22 jackals and lions all take sizeable proportions of carrion in their diet. In the spotted hyena  
23 (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*) and brown hyena (*Hyaena brunnea*) it can  
24 be over 90% (Jones et al. 2015). And although no contemporary terrestrial vertebrate exists  
25 as an obligate scavenger, most, if not all, are facultative to some extent (Beasley et al.  
26 2015). The particular reliance of hyenas on carrion means we can use them as examples of

1 efficient terrestrial scavengers to compare with other forms. In terms of locomotion, they  
2 employ a characteristic "rocking horse gait" which allows them to cover great distances  
3 efficiently, loping at 10 km/hr (Mills 1989, Jones et al. 2015). Such long-distance travel is  
4 apparent in African wild dogs (*Lycaon pictus*) and many other canids (Pennycuick 1995,  
5 Janis and Figueirido 2014). In contrast, big cats like leopards (*Panthera pardus*) rely on  
6 ambush (Pennycuick 1995). This allows us to make a broad distinction between the ambush  
7 strategies of cat-like forms and the pursuit/ pounce strategies of more dog-like forms, the  
8 latter being more suited to scavenging (Janis and Figueirido 2014). These insights allow us  
9 to compare extant terrestrial species to their prehistoric forebears given the dominance of  
10 mammalian carnivores since the Eocene (56-33.9 Mya) where the order split into the  
11 Caniforma and Feliforma (Van Valkenburgh 1987). To take one example, Anyonge (1996)  
12 found that *Nimravides*, a genus of sabretooth cat from the Miocene (10.3 to 5.3 Mya), were  
13 likely to have been ambush predators which would argue against them taking a lot of carrion.

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

26 Aside from humans and our allies, the best-known terrestrial bipeds are the dinosaurs and

1 unsurprisingly, given their enduring appeal, the prevalence of scavenging has been extensively  
2 explored in the carnivorous theropods. These were the dominant terrestrial carnivores for  
3 most of the Mesozoic Era (252.17 - 66 Mya) and ranged from the chicken-sized to the  
4 whale-sized, all of which were bipedal. While the locomotory ability of theropods has been  
5 debated since their first inception, more recent studies have reconstructed them as relatively  
6 mobile animals (Pontzer et al. 2009). Despite some suggestions that larger species may have  
7 had some advantage in scavenging, partially due to the ability to search large areas (Ruxton  
8 and Houston 2003), more recent studies have shown that the energetic demands of such  
9 large forms meant scavenging was likely more prevalent in mid-sized theropods of  
10 approximately half a tonne (Carbone et al. 2011, Kane et al. 2016)

## 11 **Detection**

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

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

1 Ruxton and Houston (2004b) to be able to survive as a scavenger.

2 Indeed, the olfactory senses of many extant (and in all probability extinct) carnivores meet  
3 this required distance, making scavenging feasible for most terrestrial carnivores (Farlow  
4 1994, Mech and Boitani 2010). Among extinct species in particular, we can use the ratio of  
5 olfactory bulb to brain size to infer a preference for olfactory foraging (Zelenitsky et al.  
6 2011). This approach was used by Zelenitsky et al. (2011) to hypothesise such a mode for  
7 the theropod dinosaur *Bambiraptor* and by Witmer and Ridgely (2009) for tyrannosaurs. The  
8 flying pterosaurs however, had tiny olfactory bulbs indicating this sense was not relied on  
9 (Witton 2013)

10 Species capable of flight have effectively added an extra spatial dimension (i.e. the  
11 vertical component) to their sensory environment over land animals. This allows them to look  
12 down on a landscape where they are unencumbered by obstacles that would obstruct the view  
13 of a terrestrial scavenger. Such an ability has obvious benefits in detecting carrion. Certainly,  
14 vultures are known to have impressive visual acuity, with one estimate indicating lappet-faced  
15 vultures (*Torgos tracheliotus*) are capable of detecting a 2 metre carcass over 10 km away  
16 (Spiegel et al. 2013). Eagles too are known to have highly developed vision (Reymond 1985).  
17 It follows that the evolution of flight allowed aerial animals to detect far more carrion than  
18 their terrestrial counterparts through vision (Lisney et al. 2013) as the pterosaurs  
19 convergently evolved large orbits and optic lobes (Witton 2013).

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

1 successful forager. Thus, it seems probable that scrounging behaviours were seen in the flying  
2 pterosaurs as well.

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

9 Although aquatic species also have a vertical component because they forage in a water  
10 body, they must contend with the low-light environment where visual detection distances are  
11 far lower ( $< 100$  m) than they would be for air. As such, aquatic animals detect resources  
12 through chemo- and mechanoreception more so than through vision (Ruxton and Houston  
13 2004a). This is particularly relevant to sharks and aquatic snakes who are deemed as having  
14 the most suitable physiology for scavenging. A hypothesis put forth by Sazima and  
15 Strüssmann (1990) argued that chemical gradients in water would allow for a relatively easier  
16 detection of carrion by snakes. This gained some support from DeVault and Krochmal  
17 (2002), who found a preponderance of aquatic snake species in their review of this behaviour.  
18 Smell seems to be the primary means of carcass detection in sharks as well. Fallows et al.  
19 (2013) found that wind speed determined the number of sharks feeding at whale carcasses,  
20 indicating they were dependent on detecting the odours from the decaying whales.

## 21 **Handling Time**

22 Since the food a scavenger depends upon is not dispatched directly, often the most easily  
23 accessible and choicest components of the carcass will be missing or, if present, will be  
24 subject to decay as well as competition. So being able to overcome competitors and

1 maximise the nutrient gain from the remnants are all essential parts of carcass handling time.

2 We will first consider the adaptations to defeating competitors.

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

9 We would expect this trait to be selected for even in the case of weight-constrained,  
10 scavenging fliers. This is true for wandering albatrosses (*Diomedea exulans*), cinereous  
11 vultures (*Aegypius monachus*) and condors (*Vultur gryphus*, *Gymnogyps californianus*) who  
12 all have body masses that can exceed 10 kg and represent some of the heaviest bird species  
13 capable of flight (Weimerskirch 1992, Ferguson-Lees and Christie 2001, Donazar et al. 2002).  
14 Indeed, such is the competitive advantage held by vultures over other facultative scavenging  
15 birds that temporal niche partitioning at the carcass has evolved (Kendall 2013, Kane et al.  
16 2014). Additionally, many pterosaurs were far bigger again, with estimated body masses of  
17 over 200 kg in the Azhdarchids (Witton and Habib 2010). Although Witton and Naish  
18 (2008) argued that neck inflexibility and straight, rather than hooked jaw morphology points  
19 against Azhdarchids existing as *obligate* scavengers, their terrestrial proficiency indicates they  
20 would have been comfortable foraging on the ground. Extant Marabou Storks (*Leptoptilos*  
21 *crumenifer*) have a comparable morphology and are noted facultative scavengers (Monadjem  
22 et al. 2012) so it is reasonable to believe that these pterosaurs behaved similarly.

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

2013).

In addition to fending off other vertebrates, scavengers also have to contend with competition from microorganisms, 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 microorganism 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 ectotherms 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).

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 carcasses, 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 20 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

1 muscle tissue, it makes skeletal remains an enticing resource (Brown 1989). This ability  
2 reached its zenith among hyenas with the evolution of the estimated 110 kg *Pachycrocuta*  
3 *brevirostris* during the Pliocene (3.6 - 2.58 Mya; Palmqvist et al. 2011). Indeed, their  
4 extinction has been blamed on the decline of sabretooth cats (Machairodontinae), the unique  
5 skull morphology of the latter meant they would leave a large amount of food on a carcass  
6 for would-be scavengers (Palmqvist et al. 2011). Earlier in the evolution of mammals, the  
7 bone-crushing dogs that evolved during the Oligocene (Borophaginae; 33.9 - 23.03 Mya)  
8 have also been compared to hyenas in terms of their feeding ecology (Van Valkenburgh et al.  
9 2003, Martín-Serra et al. 2016).

10 In Mesozoic systems some large theropod dinosaurs had a morphology indicative of an  
11 ability to process bone (e.g. the robust skull and dentition of *Tyrannosaurus rex* Hone and  
12 Rauhut 2010). There is direct evidence that *T. rex* did this in the form of distinctive wear  
13 marks on its tooth apices (Farlow and Brinkman 1994, Schubert and Ungar 2005) and the  
14 presence of bone fragments in its coprolites (Chin et al. 1998). The animal also had an  
15 enormous bite force, with one estimate putting it at 57000 Newtons (Bates and Falkingham  
16 2012) which would have been powerful enough to break open skeletons (Rayfield et al. 2001).

17 Despite not having the anatomical ability to break open bone, the bearded vulture  
18 (*Gypaetus barbatus*) has evolved a technique whereby it drops long bones from a height,  
19 splintering them on the rocks below which allows them to feed (Margalida 2008). Similarly,  
20 early hominins developed the ability to craft tools for breaking open bones (Blasco et al.  
21 2014). A recent study investigating potential scavenging opportunities for hominins in Kenya  
22 found that, in addition to skeletal material, there is a substantial amount of scavengeable  
23 meat left on predated remains; sufficient to sustain the requirements of an adult male *Homo*  
24 *erectus* (Pobiner 2015). In some historical hominin-inhabited areas there were a greater  
25 number of felids than hyenids. Again, this is significant because hyenas are likely to have left  
26 far less flesh on a carcass than a felid such as a sabretooth, enabling contemporaneous



1 hominins to benefit (Pobiner 2015). The use of tools and the cooperative nature of hominins  
2 meant they could likely get a substantial part of their energetic requirements through  
3 scavenging depending on their environment (Moleón et al. 2014).

4 On the ground, and despite the advantages of social resource defence, the competitive  
5 ability of even the largest flying bird is radically diminished in their interactions with  
6 mammalian competitors, and as such they tend to consume carrion rapidly. Houston (1974)  
7 observed a group of *Gyps* vultures consuming all of the soft tissue from a 50 kg Grant's  
8 gazelle (*Nanger granti*) in eight minutes. Their serrated tongues and hooked bills enabling  
9 them to achieve this feat (Houston and Cooper 1975). Aside from raptors, the specialised  
10 beaks of many modern bird lineages tends to hinder their ability to eat meat which is in  
11 contrast to the first lineages that did not have this feature (Martyniuk 2012). As Martyniuk  
12 (2012) notes these early birds would thus have been predominantly carnivorous, implying  
13 scavenging was a live opportunity cf. their descendants. Among the pterosaurs, Witton  
14 (2013) makes the case that the istiodactyl pterosaurs were the most likely scavengers of this  
15 group based on their potential handling time. The mix of strong and weak features in their  
16 skull morphology is indicative of animals that were suited to removing large amounts of flesh  
17 from an immobile foodstuff (Witton 2013).

18 Some clades appear to lack many, if not all, of the phenotypic adaptations associated  
19 with an efficient carcass handling time. For example, the extant bats seem to lack all of the  
20 features we have identified as important. The larger forms (which are better suited for  
21 scavenging, following our previous arguments) are typically frugivores and therefore lack the  
22 adaptations for digesting meat while the smaller carnivorous bats are mainly found in the  
23 microbats, which are insectivorous (Aguirre et al. 2003). Additionally, their poor terrestrial  
24 ability and cost of movement on the ground would also count against them while attempting  
25 to fend off competitors at a carcass (Riskin et al. 2006, Voigt et al. 2012). That said,  
26 *Necromantis* ("death-eater"), a large bat from the middle to late Eocene (56-33.9 Mya) had

1 a robust cranio-mandibular morphology, and is a likely candidate for an extinct scavenging  
2 bat (Weithofer 1887, Hand et al. 2012)

3 The support of water allows for many aquatic species to reach large sizes thus granting its  
4 benefits. Collins et al. (2005) found "contrasting relationships between size (body mass) and  
5 depth in the scavenging and predatory demersal ichthyofauna". Predatory species saw a  
6 reduction in body mass with depth whereas the reverse trend was true for scavengers. This,  
7 the authors pointed out, is because randomly distributed carrion is better exploited by fish  
8 with larger body sizes owing to starvation resistance.

9 Certainly, scavenging should be particularly attractive to flying species compared to  
10 mammals. The latter can kill prey up to the same body mass as themselves and sometimes  
11 an order of magnitude heavier (e.g. socially hunting lions; Owen-Smith and Mills 2008). In  
12 contrast, birds of prey tend to kill prey smaller than themselves (Slagsvold and Sonerud 2007)  
13 because of the greater cost of injury and the need to carry off their food. Scavenging  
14 provides a means for birds to exploit species that would otherwise be too big for them to kill.

15 Because of the random nature of carrion we would expect adaptations that reduce  
16 energetic costs of maintenance to be selected for in scavengers as it would maximise the  
17 benefit derived from such a sporadic food source. Extant reptiles possess an advantage here,  
18 in that over the course of a year their food requirements can be 30 times lower than an  
19 endotherm of equal size (Nagy 2005). DeVault and Krochmal (2002) suggest this is an  
20 avenue for scavenging in snakes because they "exhibit exceedingly low maintenance  
21 metabolisms, and most can survive on a few scant feedings per year. It is, therefore, possible  
22 for snakes to rely largely on infrequent, less energy-rich meals." In the same review the  
23 authors found occurrences of scavenging spread across five families of snakes and stated that  
24 this behaviour is "far more common than currently acknowledged." (DeVault and Krochmal  
25 2002). The same reasoning can be applied to crocodiles and their allies (Forrest 2003)  
26 because a sit and wait strategy is viable for an ectotherm.

## 1 Prey Availability

2 The position of a species on the scavenging scale can also be influenced by the availability of  
3 carrion in the environment, which is dependent on biotic and abiotic factors. Aspects  
4 including, primary productivity, relief, temperature and competition will all greatly affect  
5 scavenging tendency. Ruxton and Houston (2004b) suggest a system with a productivity  
6 similar to the Serengeti could have supported an obligate mammalian or reptilian terrestrial  
7 scavenger. Indeed, in systems that were dominated by large ectothermic or mesothermic  
8 herbivore vertebrates, the same primary productivity would have supported a greater biomass,  
9 due to the scaling of mass with metabolic rate (McNab 2009). The upshot of this is that  
10 there was a higher biomass of herbivores dying and offering scavenging opportunities.  
11 Predators were large-bodied too compared to extant mammalian predators (McNab 2009),  
12 and so, especially if they were ectothermic, could last longer between meals, rendering  
13 scavenging a more attractive behaviour relative to predation. Osteophagy may have been  
14 even more viable during the Mesozoic era as well because of this skewed body mass  
15 distribution of herbivores towards larger sizes (O’Gorman and Hone 2012). When we couple  
16 this with the fact that skeletal mass scales greater than linearly with body mass (Prange  
17 et al. 1979) there would have been a lot of bone material to consume in the environment  
18 provided an animal had the biology to process it (Chure and Fiorillo 1997).

19 Frequently, the interplay between abiotic and biotic factors can impact the ability of an  
20 animal to scavenge. We know vultures and eagles tend to soar using thermals and if these air  
21 pockets don’t form, say on a cloudy day, the bird is grounded (Mundy et al. 1992). In many  
22 habitats (e.g. the Arctic) it is simply not possible for sufficiently powerful thermals to form  
23 and as a consequence large-bodied vultures cannot exist. One result of this is that terrestrial  
24 carnivores like bears and wolves take more carrion (DeVault et al. 2003). Certainly, a major  
25 difficulty for terrestrial scavengers is competition with vultures. Nocturnal behaviour in the

hyaenidae in general has been put forth as an adaptation to reduce competition with these exclusively diurnal birds (Gittleman 2013). If we apply this line of reasoning over evolutionary time-scales, the absence of flying vertebrates in the Palaeozoic may have permitted terrestrial forms to take in a higher proportion of carrion in their diet.

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 ichthyosaurs, that could all exceed 15 metres in length (Ruxton 2011) (reptile fall ref here).

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

1 the "dinner-bells" (Whitehead and Reeves 2005).

2 Perhaps the greatest environmental driver of scavenging tendency is that of temperature.  
3 The geological record shows the Earth has undergone radical fluctuations in temperature over  
4 time. This will have had a significant bearing on the availability and persistence of carrion.  
5 To illustrate the point, a 10°C increase in ambient temperature can double carcass  
6 decomposition rates (Parmenter and MacMahon 2009) and geological evidence indicates that  
7 the Mesozoic Earth was on average at least 6 °C warmer than now (Sellwood and Valdes  
8 2006). In terms of specific habitats, it has been shown that decomposition is greater in warm  
9 and moist areas versus more xeric ones (Beasley et al. 2015). Moreover, oceanic productivity  
10 and habitat structure are all impacted by climactic conditions. The impacts these can have  
11 on scavengers have been empirically supported e.g. Beasley et al. (2015) who point to a  
12 series of studies showing how microbes and invertebrates benefit at higher temperatures to  
13 the detriment of vertebrate scavengers such that "above 20°C vertebrates were able to detect  
14 and consume only 19% of small-mammal carcasses, whereas at temperatures below 18°C,  
15 vertebrates consumed 49% of carcasses". This is a sobering thought given the impact we  
16 humans are having on the Earth's climate.

## 17 Conclusion

18 As is often the case in science, the present provides the key to the past. The animals of  
19 today, while often different (sometimes radically so) to their ancestors, can be used to make  
20 informed comparisons to extinct species. We have used this technique to give insight into the  
21 drivers of scavenging across vertebrates through time. In common with any other forager be  
22 they grazer, browser or predator, scavengers past and present have had to balance their  
23 energetic costs with the gains of food. The main factors we considered namely, encounter  
24 rate, handling time and prey availability can be used to create a scale of scavenging

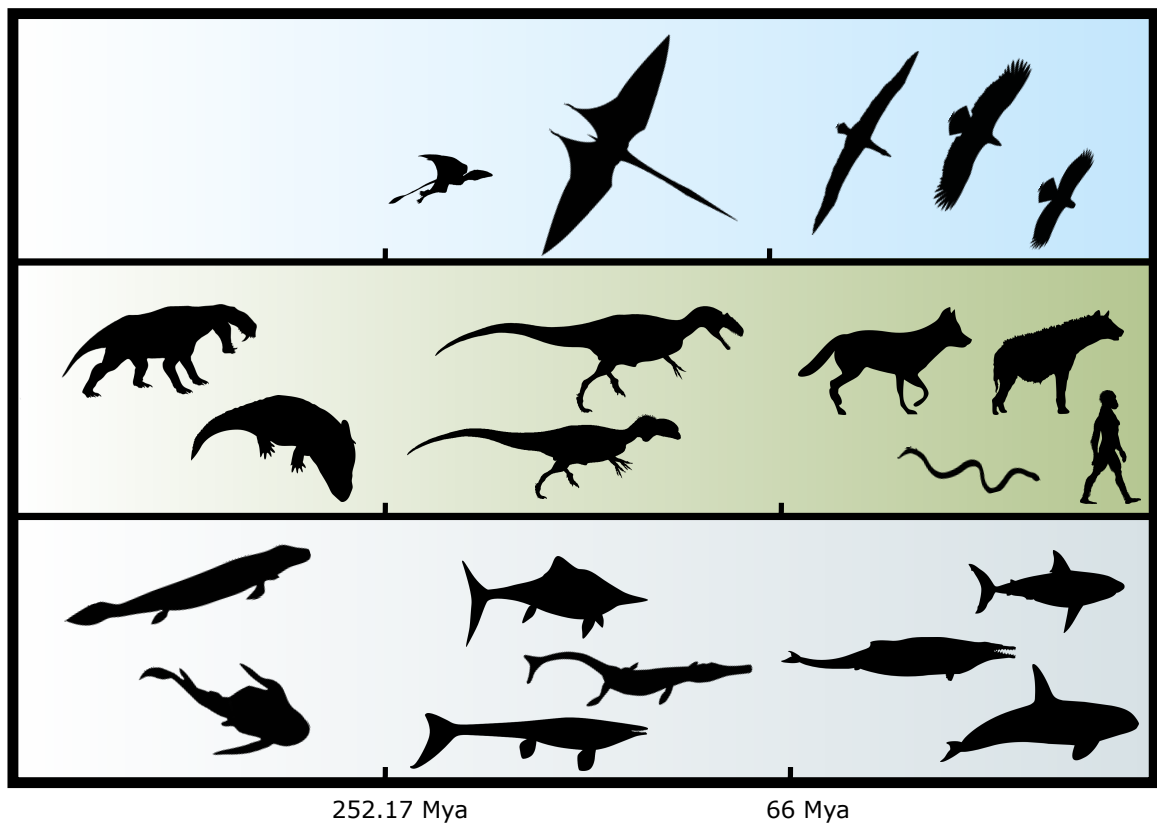


Figure 2: The diversity of scavengers through time. Each species has either direct evidence for it being a scavenger or would be positioned high up on our scavenging scale.

1 whereupon any species can be placed in order to establish the importance of carrion in it diet.  
2 We hope this approach will be useful in the effort to explore this most understudied of  
3 feeding ecologies.

## 4 **Appendix**

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

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