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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. Chief among these are low-cost locomotion, high detection distances, effective carcass processing and a carrion-producing habitat. We use these four components to highlight the morphologies and environments that would have been conducive to scavenging over geological time by focussing on 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 doesn't 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 among extinct  
14 forms. Indeed, a single species of dinosaur notwithstanding (Carbone et al. 2011), a synthesis  
15 describing the natural history of scavengers is absent from the literature. Fortunately,  
16 research on scavenging is on the rise (Koenig 2006). As a result, we are now beginning to  
17 realise the extent of this behaviour such that, "in some ecosystems, vertebrates have been  
18 documented to assimilate as much as 90% of the available carrion" (Beasley et al. 2015).  
19 This has profound implications for the trophic ecology of these systems and particularly our  
20 models of them. Even Tenney's noble big cats are now known to take in a significant portion  
21 of carrion in their diet where some lion populations get over 50% of their meat from  
22 carcasses (Jones et al. 2015). By recognising the difficulty in directly observing scavenging,  
23 other methods have been turned to to discern the most suitable morphologies, physiologies  
24 and environments for a scavenging lifestyle to prosper. Here we chart the natural history of  
25 scavenging by assessing the potential for the behaviour in dominant vertebrate groups given

1 their ecology and functional traits.

## 2 **The Difficulty of Scavenging**

3 The chief hurdle of 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 increase the probability of encountering a sufficient amount of carrion in order to meet their  
7 energetic demands. Once found, the scavenger must be able to out-compete any potential  
8 competitors and process the typically decaying carcass which contains microorganism derived  
9 toxins (Ruxton et al. 2014). Finally, the potential for scavenging will also depend on the  
10 density, size, and quality of carcasses produced, all of which are affected by complex ecosystem  
11 dynamics. All of these facets are essentially the key parameters found in functional response  
12 curves, namely encounter rate, handling time and prey availability (Jeschke et al. 2002). By  
13 considering scavenging in this context of optimal foraging we can identify the prerequisite  
14 attributes and processes required for the behaviour. This has enabled us to propose a scale of  
15 scavenging whereupon we can place any vertebrate species, past or present, and assess the  
16 importance of carrion in its diet.

## 17 **Encounter Rate**

18 All foraging processes depend on the encounter rate between the consumer and resources. In  
19 the simplest case, this rate can be thought of in terms of a gas diffusion model where the  
20 movement of two agents depends only on their relative speed. As carcasses are stationary,  
21 the relative speed between a scavenger and carrion is only dependent on the movement of the  
22 scavenger. Vertebrates do more than simply bump into resources like gas molecules though,  
23 because they can actively detect them through their sensory abilities. As such, scavenging

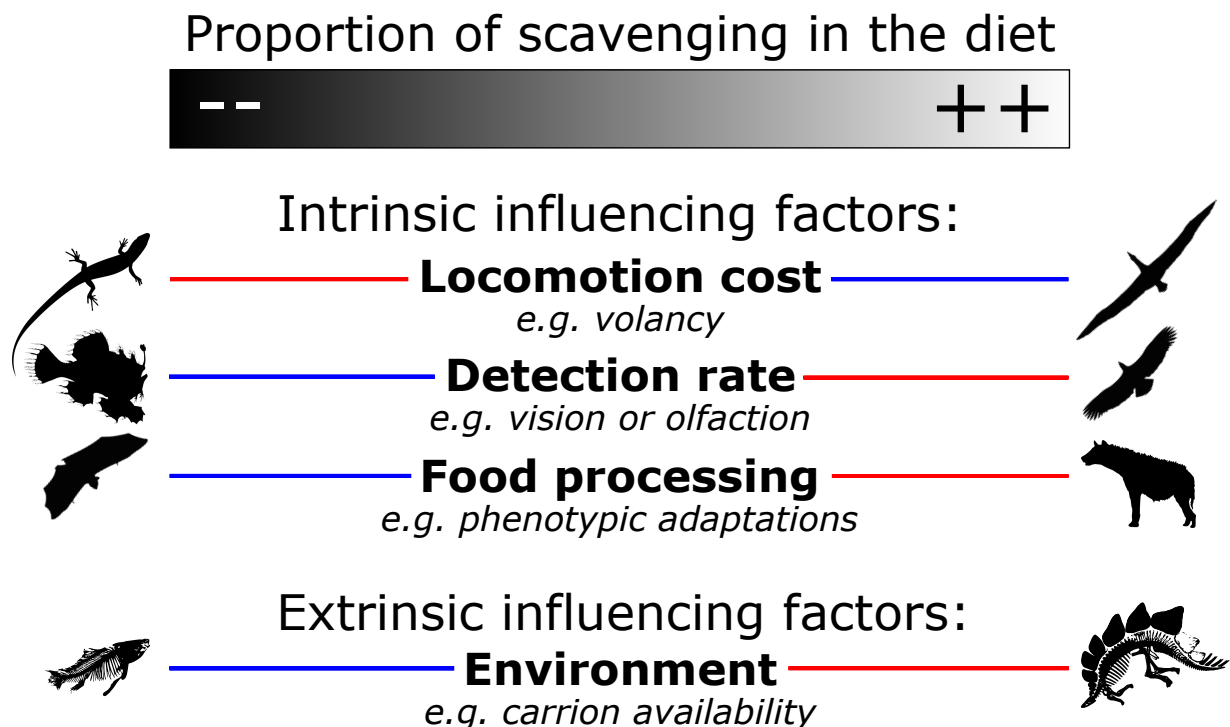


Figure 1: Factors influencing the proportion of scavenging in a vertebrates' diet. Blue lines indicates a reduction in the factor and red lines indicates an increase.

- 1 potential is strongly affected by search rates, which are determined by both species'
- 2 physiology and the dimensionality of the environment (Pawar et al. 2012).

### 3 **Locomotion**

4 Scavenging depends more on the ability to efficiently move over large areas than does

5 predation because of the inherent unpredictability of carrion. This generally requires an

6 efficient transfer of metabolic energy into movement which relies on both physiology (i.e.

7 metabolism) and the medium of the environment in which the animal is moving (i.e. aerial,

8 aquatic or terrestrial). Perhaps the most efficient form of locomotion in vertebrates is,

9 paradoxically, found in flying species. Despite the energetic costs of flight, the only known

10 vertebrate obligate scavengers are the old and the new world vultures. And, although

11 powered flight is energetically expensive, species like vultures can exploit air currents using

1 their large wingspans which allows them to soar at a cost of only twice their metabolic rate  
2 (Hedenstrom 1993, Spivey et al. 2014). By depending on thermal air flows these species can  
3 forage over vast ranges (Spiegel et al. 2013). An analagous mode of locomotion is also  
4 exploited by sea birds, which use strong ocean winds to search large areas of the oceans  
5 (Norberg 2012, Thaxter et al. 2012). While many species of seabird are likely primarily  
6 predators, it seems that albatrosses, who can range many hundreds of kilometres, take a  
7 substantial amount of carrion in their diet (Croxall and Prince 1994). This is typically in the  
8 form of squid, which float on the surface, allowing the birds to readily pluck their remains out  
9 of the water (Croxall and Prince 1994).

10 The two families from which modern vultures arose, the Accipitridae and Cathartidae,  
11 appear during the Palaeocene (66 - 56 Million years ago (Mya); Jetz et al. 2012, Jarvis et al.  
12 2014) However, soaring flight is likely to be far older than this with avian flight originating in  
13 the Late Jurassic (163.5-145 Mya) and vertebrate flight in the Late Triassic (235-201.3 Mya)  
14 coincident with the pterosaurs. Indeed, scavenging among pterosaurs has been hypothesised  
15 many times before (Witton and Naish 2008). Certain groups of these animals could reach  
16 enormous sizes (e.g. Azhdarchids with wingspans of 11 metres; Witton and Habib 2010)  
17 and, notably, appear to have engaged in soaring flight (Witton and Habib 2010). It seems  
18 that the use of soaring in extinct species as a means for scavenging is likely.

19 While soaring is perhaps the only viable means of locomotion that allows for an obligate,  
20 scavenging life-style (Ruxton and Houston 2004b), powered flight is still an efficient means of  
21 locomotion. Avian flight is cheaper than either walking or running (Tucker 1975). Even  
22 taking account of maintenance costs, this still bears out, where total cost of movement ( $J$   
23  $kg^{-1} m^{-1}$ ) scales according to  $5.2 \times \text{body mass (kg)}^{-0.23}$  for fliers and  $10.7 \times \text{body mass (kg)}$   
24  $^{-0.32}$  for runners (Williams 1999).

25 We know that many extant birds exist as facultative scavengers because storks, raptors  
26 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). 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). That said, *Necromantis* (“death-eater”), a large bat from the middle to late Eocene (56 to 33.9 Mya) had a robust cranio-mandibular morphology, and is a likely candidate for scavenging behaviour (Weithofer 1887, Hand et al. 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). In fact, the total cost of movement (again in  $\text{J kg}^{-1} \text{m}^{-1}$ ) in fish is lower than either running or flying where it scales according to  $2.15 \times \text{body mass (kg)}^{-0.25}$  (Williams 1999) with only *soaring* flight likely to surpass it. This has led some researchers to argue for the likelihood of an obligate scavenging fish (Ruxton and Houston 2004a, Ruxton and Bailey 2005). Sharks perhaps best resemble the large soaring fliers as they depend on large pectoral fins in order to maintain lift as they swim. Many shark species show very large ranges (e.g. great white sharks (*Carcharodon carcharias*)) and have the lowest cost of swimming. Facultative scavenging is seen in many marine groups including species of extant sharks such as great 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 mysticete whales from the Pliocene (Schwimmer et al. 1997, Ehret et al. 2009, 5.3 to 3.6 Mya;).

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 trajectory to fully aquatic

1 species (Williams 1999). But despite their movement away from land their energetic savings  
2 were negligible because the *total* cost incurred by a swimming marine mammal is high  
3 (Williams 1999). Indeed, the total energetic cost is similar to an equivalent terrestrial or  
4 aerial mammal (Williams 1999). This underscores the trade offs between the benefits of  
5 endothermy in terms of activity periods and the costs of maintaining such an expensive  
6 system. That said, aquatic endotherms have and do scavenge. For instance, early whales  
7 such as *Basilosaurus* seem to fit into the same niche as killer whales *Orcinus orca* and we  
8 have some evidence for scavenging in both (Fahlke 2012, Whitehead and Reeves 2005).

9 Terrestrial environments are the most energetically costly in which to move, because an  
10 animal must trade off the cost of supporting its body off the ground while propelling itself  
11 forward. The idea that the evolutionary transition in posture from the sprawling gait of  
12 reptiles to the erect posture of mammals conferred a huge advantage to the latter is often  
13 mentioned. The purported advantages include benefits in terms of speed, efficiency, muscle  
14 effort and manoeuvrability (Sullivan 2015). Yet, as Sullivan (2015) states, most of the  
15 hypotheses in favour of this idea remain to be tested in the context of archosaur evolution.  
16 Metabolic rate however, unquestionably impacts terrestrial species whereby ectotherms such  
17 as many modern reptiles, cannot move for sustained periods (Bennett and Ruben 1979). This  
18 is exacerbated by their sprawling gait which results in the phenomenon known as Carrier's  
19 constraint such that the animal can't move and breathe at the same time because the lateral  
20 movements impedes its lungs (Carrier 1987). This would also be true of extinct species. It is  
21 during the Permian (298.9 - 252.17 Mya) that we have the earliest evidence of vertebrate  
22 scavenging where a temnospondyl amphibian fed on the carcass of *Varanops*, a predatory  
23 synapsid of the time (Reisz and Tsuji 2006). Both these groups are more likely to depend on  
24 low energetic costs in order to compensate for low encounter rates due to their inability to  
25 move. It is with the evolution of endothermy in the therapsid-mammal lineage (Clarke and  
26 Pörtner 2010) that terrestrial vertebrates would have gained the ability to range more widely,



1 a vital component in seeking out carrion.

2 Modern endothermic mammals can sustain longer periods of energetically expensive  
3 activity (Bennett and Ruben 1979) resulting in larger foraging ranges. To quantify this effect  
4 with a simple example we can turn to some allometric relationships relating sustainable  
5 travelling speed to body mass (Ruxton and Houston 2004b). If we insert these into a foraging  
6 radius model (Enstipp et al. 2006) for a 12 hour foraging day it shows that while a 10 kg  
7 reptile can range 6.5 km, an equally sized mammal can range nearly 33 km . For a foraging  
8 scavenger, this ability translates into a greater area searched for food.

9 Today, terrestrial scavenging in the mammals is probably best known in an African  
10 context where hyenas, jackals and lions all take sizeable proportions of carrion in their diet.  
11 In the spotted hyena (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*) and brown hyena  
12 (*Hyaena brunnea*) it can be over 90% (Jones et al. 2015). And although no contemporary  
13 terrestrial vertebrate exists as an obligate scavenger, most, if not all, are facultative to some  
14 extent (Beasley et al. 2015). The particular reliance of hyenas on carrion means we can use  
15 them as examples of efficient terrestrial scavengers to compare with other forms. In terms of  
16 locomotion, they employ a characteristic "rocking horse gait" which allows them to cover  
17 great distances efficiently, loping at 10 km/hr (Mills 1989, Jones et al. 2015). Such  
18 long-distance travel is apparent in African wild dogs (*Lycaon pictus*) and many other canids  
19 (Pennycuick 1995, Janis and Figueirido 2014). In contrast, big cats like leopards (*Panthera*  
20 *pardus*) rely on ambush (Pennycuick 1995). This allows us to make a broad distinction  
21 between the ambush strategies of cats and the pursuit/ pounce strategies of dogs, the latter  
22 being more suited to scavenging (Janis and Figueirido 2014). We can (and have) use(d)  
23 these insights to compare extant terrestrial species to their prehistoric forebears given the  
24 dominance of mammalian carnivores since the Eocene (56-33.9 Million years ago; Mya) where  
25 the order split into the Caniforma and Feliforma (Van Valkenburgh 1987). To take one  
26 example, Anyonge (1996) found that *Nimravides*, a genus of sabretooth cat from the

1 Miocene (10.3 to 5.3 Mya) were likely to have been ambush predators which would argue  
2 against them taking a lot of carrion.

3 The evolution of bipedal movement freed up the forelimbs for other purposes e.g. wings,  
4 tool-use etc. In terms of its cost Alexander (2004) shows that, in the case of humans, we are  
5 more economical than predicted while walking and less so while running.

6 Unsurprisingly, given their enduring appeal, the prevalence of scavenging has been  
7 explored in the carnivorous, theropod dinosaurs. They were the dominant terrestrial  
8 carnivores for most of the Mesozoic Era (252.17 - 66 Mya) and ranged from the chicken-sized  
9 to the whale-sized, all of which were bipedal. They are quite alien to anything we know today  
10 which restricts our ability to understand their ecology far more so than extinct mammals  
11 (Weishampel et al. 2004). Of relevance, are the questions that still persist about their  
12 metabolism, with the latest evidence suggesting they were mesothermic i.e. intermediate to  
13 ecto- and endotherms (Grady et al. 2014). We do know that they walked with the erect gait  
14 of mammals or birds rather than the sprawling gait of lizards and that they were most likely  
15 facultative scavengers (Weishampel et al. 2004, DePalma et al. 2013). Taken together, this  
16 implies dinosaurs had a foraging range that fell in between that of modern terrestrial  
17 mammals and reptiles.

## 18 **Detection**

19 It would be pointless to have incredible ranging abilities and not have the sensory architecture  
20 to benefit from it. As predicted by the necessity of an increased encounter rate, scavengers  
21 have well-developed detection senses. A simplification of terrestrial, vertebrate scavengers in  
22 sensory terms is one of them existing in a two-dimensional plane while foraging for carrion  
23 directly. They can detect carcasses at a range that is defined by the radius of their sensory  
24 organs. As a consequence, they have a much more restricted view of the landscape than do  
25 aerial foragers. Hyenas make up for this in their ability to smell a rotting carcass 4 km away

1 and to hear the vocalisations of conspecifics at a distance of 10 km (Mills 1989). If we  
2 compare this to the energetics approach by Ruxton and Houston (2004b), they calculated a  
3 terrestrial scavenger needs to be able to detect carrion at 500 meter in order to survive,  
4 which is clearly within the ability of hyenas. Moreover, the senses of many extant (and in all  
5 probability extinct) carnivores meet this required distance, making scavenging feasible for  
6 terrestrial species (Farlow 1994, Mech and Boitani 2010).

7 Species capable of flight have effectively added an extra spatial dimension, i.e. the  
8 vertical component, to their sensory environment over land animals. This allows them to look  
9 down on a landscape where they are unencumbered by obstacles that would obstruct the view  
10 of a terrestrial scavenger. Such an ability has obvious benefits in detecting carrion. Certainly,  
11 vultures are known to have impressive visual acuity, with one estimate indicating lappet-faced  
12 vultures (*Torgos tracheliotus*) are capable of detecting a 2 metre carcass over 10 km away  
13 (Spiegel et al. 2013). Eagles too are known to have highly developed vision (Reymond 1985).  
14 It follows that the evolution of flight allowed aerial animals to detect far more carrion than  
15 their terrestrial counterparts (Lisney et al. 2013). We can contrast this with many bats whose  
16 reliance on echolocation would not lend itself to discovering immobile carrion.

17 Having a panoramic view also means being able to gather a wealth of information from  
18 other foragers, be they conspecifics or otherwise (Jackson et al. 2008). Again, returning to  
19 vultures, the genus *Gyps* consists of highly social and colonially nesting species  
20 (Fernández-Bellon et al. 2015). These behaviours allow them forage far more efficiently  
21 because one bird can scrounge information on the location of food from another successful  
22 forager (Kane et al. 2014).

23 Aside from sight, many birds have well developed olfactory systems (Lisney et al. 2013)  
24 including three species of vultures within the new world family Cathartidae, (genus  
25 *Cathartes*). Among them are the Turkey Vultures (*Cathartes aura*) which were able to locate  
26 90% of baits set out in a tropical forest (Houston 1986). An atuned sense of smell is

1 obviously useful in detecting decaying carrion from the air.

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

## 14 Handling Time

15 Since carrion is not dispatched directly, often the most easily accessible and choicest  
16 components of the carcass will be missing or, if present, will be fought over. Being able to  
17 extract nutrients from remnants gives a scavenger a great advantage. Thus, some phenotypic  
18 adaptations such as the ability to crush bone (as seen in hyenas) reveals another useful  
19 scavenger trait. Osteophagy is known across a range of terrestrial carnivores and given that  
20 some fat-rich mammalian bones have an energy density (6.7 kJ/g) comparable with that of  
21 muscle tissue, it makes skeletal remains an enticing resource (Brown 1989). This ability  
22 reached its zenith among hyenas with the evolution of the 110 kg *Pachycrocuta brevirostris*  
23 during the Pliocene (3.6 - 2.58 Mya; Palmqvist et al. 2011). Indeed, their extinction has  
24 been blamed on the decline of sabretooth cats (Machairodontinae), the unique skull

1 morphology of the latter meant they would leave a large amount of food on a carcass for  
2 would-be scavengers (Palmqvist et al. 2011). Earlier in the evolution of mammals, the  
3 bone-crushing dogs that evolved during the Oligocene (Borophaginae; 33.9 - 23.03 Mya)  
4 have also been compared to hyenas in terms of their feeding ecology (Van Valkenburgh et al.  
5 2003, Martín-Serra et al. 2016).

6 Interestingly, such comparisons have given insight into the feeding ecology of early  
7 hominins who, for instance, had the ability to craft tools for breaking open bones (Blasco  
8 et al. 2014). The question of where our ancestors placed on the hunter-scavenger axis during  
9 the Plio-Pleistocene has been a matter of debate for years (Domínguez-Rodrigo 2002). A  
10 recent study investigating potential scavenging opportunities for hominins in Kenya found  
11 that, even when discounting bone material, there is a substantial amount of scavengeable  
12 meat left on predated remains; sufficient to sustain the requirements of an adult male *Homo*  
13 *erectus* (Pobiner 2015). In some historical hominin-inhabited areas there were a greater  
14 number of felids than hyenids. Again, this is significant because hyenas are likely to have left  
15 far less flesh on a carcass than a felid such as a sabretooth enabling contemporaneous  
16 hominins to benefit (Pobiner 2015). The use of tools and the cooperative nature of hominins  
17 meant they could likely take a certain part of their energetic requirements from carrions  
18 depending on their environment (Moleón et al. 2014).

19 In Mesozoic systems some extremely large theropod dinosaurs had a morphology  
20 indicative of an ability to process bone e.g. the robust skull and dentition of *Tyrannosaurus*  
21 *rex* (Hone and Rauhut 2010). There is direct evidence that *T. rex* did this in the form of  
22 distinctive wear marks on its tooth apices (Farlow and Brinkman 1994, Schubert and Ungar  
23 2005) and the presence of bone fragments in its coprolites (Chin et al. 1998). The animal  
24 also had an enormous bite force, with one estimate putting it at 57000 Newtons (Bates and  
25 Falkingham 2012). This is noted as being powerful enough to break open skeletal material  
26 (Rayfield et al. 2001).

1 Further, much work has focused on the existence of scavenging in dinosaurs by using  
2 simple energetics approaches that typically focused on a single species namely *T. rex* (Ruxton  
3 and Houston 2003, Carbone et al. 2011) but a recent modelling study investigated the likely  
4 prevalence of scavenging across a range of body sizes. In it the authors demonstrated that  
5 species of intermediate body masses (approximately 500 kg) would have gained the most  
6 benefit from scavenging. This was the result of gut capacity limitations and the effects of  
7 competition at the carcass. At the larger extreme this owes to the fact that gut capacity  
8 doesn't scale isometrically with body mass so the benefits of greater mass level off; there's  
9 only so much food an individual can consume at a single sitting (Calder 1996). For the  
10 smaller species, larger competitors would have prevented their access to carrion.

11 In addition to reducing locomotory costs we would expect adaptations that reduce  
12 energetic costs of maintenance to be selected for in scavengers because it would maximise  
13 the benefit derived from such a sporadic food source. Extant reptiles possess an advantage  
14 here, in that over the course of a year their food requirements can be 30 times lower than an  
15 endotherm of equal size (Nagy 2005). DeVault and Krochmal (2002) suggest this is an  
16 avenue for scavenging in snakes because they "exhibit exceedingly low maintenance  
17 metabolisms, and most can survive on a few scant feedings per year. It is, therefore, possible  
18 for snakes to rely largely on infrequent, less energy-rich meals." In the same review the  
19 authors found occurrences of scavenging spread across five families of snakes and stated that  
20 this behaviour is "far more common than currently acknowledged." (DeVault and Krochmal  
21 2002). The same reasoning can be applied to crocodiles and their allies (Forrest 2003). A sit  
22 and wait strategy is viable for an ectotherm. This low existence cost is also realised in many  
23 sharks who have coupled low locomotory costs with an ectothermic metabolism. The upshot  
24 is that 30 kg of blubber can sustain a white shark for over six weeks (Carey et al. 1982).

25 Large body size confers substantial dominance and starvation-resistance benefits (Ruxton  
26 and Houston 2004b). Thus, we would expect scavengers to have this trait selected for even

1 in the case of weight-constrained fliers. Wandering Albatrosses (*Diomedea exulans*),  
2 cinereous vultures (*Aegypius monachus*) and condors (*Vultur gryphus*, *Gymnogyps*  
3 *californianus*) all have body masses that can exceed 10 kg and represent some of the heaviest  
4 bird species capable of flight (Weimerskirch 1992, Ferguson-Lees and Christie 2001, Donázar  
5 et al. 2002). And as we have noted the Azhdarchid pterosaurs were far bigger again, with  
6 estimated body masses of over 200 kg (Witton and Habib 2010). Although Witton and Naish  
7 (2008) argued that neck inflexibility and straight, rather than hooked jaw morphology points  
8 against pterosaurs existing as *obligate* scavengers, Azhdarchid terrestrial proficiency indicates  
9 they would have been comfortable foraging on the ground. Indeed, extant Marabou Storks  
10 (*Leptoptilos crumenifer*) have a comparable morphology and are noted facultative scavengers  
11 (Monadjem et al. 2012) so it is reasonable to believe that certain pterosaurs behaved  
12 similarly.

13 Certainly, scavenging should be particularly attractive to flying species compared to  
14 mammals. The latter can kill prey up to the same body mass as themselves and sometimes  
15 an order of magnitude heavier (e.g. socially hunting lions; Owen-Smith and Mills 2008). In  
16 contrast, birds of prey tend to kill prey smaller than themselves (Slagsvold and A Sonerud  
17 2007) because of the greater cost of injury and the need to carry off their food. Scavenging  
18 provides a means for birds to exploit species that would otherwise be too big for them to kill.

19 On the ground, the competitive ability of even the largest flying bird is radically  
20 diminished in their interactions with mammalian competitors however, and as such they tend  
21 to consume carrion rapidly. Houston (1974) observed a group of *Gyps* vultures consuming all  
22 of the soft tissue from a 50 kg Grant's gazelle (*Nanger granti*) in eight minutes. Their  
23 serrated tongues and hooked bills enabling them to achieve this feat (Houston and Cooper  
24 1975). Outside of raptors such as vultures, the specialised beaks of many modern bird  
25 lineages hinders their ability to eat meat which is in contrast to the first lineages that did not  
26 have this feature (Martyniuk 2012). As Martyniuk (2012) notes these early birds would thus

1 have been predominantly carnivorous, which implies that scavenging would have been a live  
2 opportunity cf. their descendants.

3 Although the findings of Shivik (2006) that “evolutionary pressures favor detection  
4 maximizers relative to toxification minimizers in competitive interactions for carcasses.”  
5 appears sound, the fact remains that overcoming microorganism toxins is still a beneficial  
6 adaptation to any scavenger. Avian scavengers have evolved incredibly acidic stomachs that  
7 allow them to consume and process putrefied flesh with no ill effects (Houston and Cooper  
8 1975, Roggenbuck et al. 2014). This adaptation is not restricted to vultures though,  
9 Grémillet et al. (2012) showed wandering albatrosses (*Diomedea exulans*; so-called “vultures  
10 of the seas”) had an average pH of 1.5, which enables them to consume fisheries discards  
11 and squid carcasses. There is also evidence of selection for “toxification minimizers” beyond  
12 birds among the ectotherms. From our earlier arguments we know that ectotherms are  
13 limited in their ability to find carrion as quickly as endotherms. This implies later arrivers  
14 would benefit especially from well-developed detoxifying apparatus. Shivik (2006) suggests  
15 that “specialized oral structures in snakes may have evolved under pressures associated with  
16 scavenging.” Moreover, some researchers have suggested an evolutionary course from basal  
17 fossorial snakes to modern terrestrial species by way of an obligate scavenger intermediate  
18 (Bauchot 2006).

19 Conversely, entire clades appear to lack many, if not all, of these phenotypic adaptations.  
20 For example, the extant bats appear to lack most of the features we have identified as  
21 important in reducing handling time. The larger forms (which are better suited for  
22 scavenging, following our previous arguments) are typically frugivores and therefore lack the  
23 adaptations for digesting meat. While the smaller carnivorous bats are mainly found in the  
24 microbats which are insectivorous (Aguirre et al. 2003). Additionally, their poor terrestrial  
25 ability would also count against them when feeding at a carcass (Riskin et al. 2006).



## Prey Availability

The position of a species on the scavenging scale can also be influenced by the availability of carrion in the environment, which is dependent on biotic and abiotic factors. Aspects including, primary productivity, relief, temperature and competition will all greatly affect scavenging tendency. Ruxton and Houston (2004b) suggest a system with a productivity similar to the Serengeti could have supported a mammalian or reptilian terrestrial scavenger. Indeed, in systems that were dominated by large ectothermic or mesothermic vertebrates, the same primary productivity would have supported a greater biomass (McNab 2009). The upshot of this is that there was a higher biomass of herbivores dying and offering scavenging opportunities. Predators were large-bodied too compared to extant mammalian predators (McNab 2009), and so, especially if they were ectothermic, could last longer between meals, rendering scavenging a more attractive behaviour relative to predation. 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).

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

1 exclusively diurnal birds (Gittleman 2013). If we apply this line of reasoning over evolutionary  
2 time-scales, the absence of flying vertebrates in the Palaeozoic may have permitted terrestrial  
3 forms to take in a higher proportion of carrion in their diet.

4 In fact, scavenging behaviour may have evolved on land as soon as the first terrestrial  
5 tetrapods emerged. Some of the earlier tetrapods tracks dating back to the early Middle  
6 Devonian (393.3 - 387.7 Mya) were found in intertidal environments (Niedzwiedzki et al.  
7 2010). These environments are isolated from marine systems twice a day leaving potential  
8 carrion unexploited by marine vertebrates. Niedzwiedzki et al. (2010) suggest that these  
9 environments “would thus have allowed marine ancestors of tetrapods gradually to acquire  
10 terrestrial competence while accessing a new and essentially untouched resource.”

11 Staying in the aquatic setting, the phenomenon of occasional bounties of carrion in the  
12 form of whale falls has led some researchers to investigate if a scavenger could survive by  
13 seeking out these remains exclusively. Ruxton and Bailey (2005) argued that although this is  
14 energetically feasible it's ecologically unlikely. Any animal that could find such whale  
15 carcasses is unlikely to have ignored other types of carrion. Although no aquatic species have  
16 ever exceeded the size of whales, some enormous animals have evolved in this environment  
17 before the evolution of whales, including *Leedsichthys*, a bony fish from the Middle Jurassic  
18 (174.1-163.5 Mya), that weighed in excess of 20 tonnes. Thus, the energetic feasibility of a  
19 marine scavenger that specialises on large carcasses has a long history. One point of interest  
20 is that of the whaling industry, which provided a bonanza of floating carcasses especially  
21 during the 20th century (Whitehead and Reeves 2005). This meant killer whales could switch  
22 from hunting to scavenging, a switch made that much easier by the noise of the whaling  
23 vessels that would effectively ring the “dinner-bells” (Whitehead and Reeves 2005).

24 Perhaps the greatest environmental driver of scavenging tendency is that of temperature.  
25 The geological record shows the Earth has undergone radical fluctuations in temperature over  
26 time. This will have had a significant bearing on the availability and persistence of carrion.

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

## 13 Conclusion

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

## 1 **Appendix**

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

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