

1 **Running title:** Scavenging in vertebrates

2 **Number of words:** ~9999

3 **Date of submission:** March 23, 2016

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

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Abstract

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

Introduction

Historically, scavengers have not been viewed as the most charismatic of animals. This may go some way to explaining the gap in our knowledge of the prevalence of this behaviour. Consider Professor Sanborn Tenney writing in 1877 for *The American Naturalist* who had this to say about one well known group, "Prominent among the mammalian scavengers are the hyenas, the ugliest in their general appearance of all the flesh eaters." He contrasts these with "nobler kinds" of carnivores such as lions and tigers (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 doesn't only feed on animals too big for it to have hunted. The obvious lack of direct behavioural data compounds the difficulty of discerning scavenging among extinct forms. Indeed, a single species of dinosaur notwithstanding, a synthesis describing the natural history of scavengers is absent from the literature. Fortunately, research on scavenging is on the rise (Koenig 2006). As a result, we are now beginning to realise the extent of this behaviour such that, "in some ecosystems, vertebrates have been documented to assimilate as much as 90% of the available carrion" (Beasley et al. 2015). Even Tenney's noble big cats are now known to take in a significant portion of carrion in their diet where some lion populations get over 50% of their meat from carcasses. By recognising the difficulty in directly observing scavenging, a suite of methods have been used to discern the most suitable morphologies, physiologies and environments for a scavenging lifestyle to prosper. Here we chart the natural history of scavenging by looking at the potential for the behaviour in dominant vertebrate groups.

The Difficulty of Scavenging

The chief hurdle to scavenging is finding a sufficient quantity of food, the occurrence of which is difficult to predict in space and time. Thus, any animal existing as a scavenger must minimise its locomotory costs and maximise its detection capabilities (Ruxton and Houston 2004b). Once found, the scavenger has to process the carrion and overcome the agents of decay produced by the action of microorganisms on the carcass (Ruxton et al. 2014). The habitat must also be productive enough to sustain an animal biomass that will eventually produce carcasses. We can draw on the image of a scavenger moving through its environment, searching for food and trying to process it efficiently as we explore the prevalence of this behaviour through time.

Locomotion

As endotherms, mammals can sustain long bouts of energetically expensive activity. By contrast, modern reptiles are ectothermic, limiting their activity periods. This is exacerbated by the sprawling gait seen in many lizards which results in Carrier's Constraint such that the animal can't move and breathe at the same time because the lateral movements impedes its lungs (Carrier 1987). An effect which manifests itself in aspects such as maximum sustainable speed where an equivalent mammal has a six to seven fold increase (Ruben 1995). To quantify this effect with a simple example we can turn to some allometric relationships relating sustainable travelling speed to body mass. In the case of mammals and reptiles these are $1.15 * \text{body mass (kg)}^{0.12}$ and $0.23 * \text{body mass (kg)}^{0.12}$ respectively (Ruxton and Houston 2004b). We can insert these into a foraging radius model $((\text{duration} * \text{speed})/2)/1000$ for a 12 hour foraging day which shows that while a 10 kg reptile can range 6.5 km an equally sized mammal can range nearly 33 km (Enstipp et al. 2006).

Today, terrestrial scavenging in the mammals is probably best known in an African

context where hyenas, jackals and lions all take sizable proportions of carrion in their diet. In the spotted hyena (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*) and brown hyena (*Hyaena brunnea*) it can be over 90% (Jones et al. 2015). Yet, no contemporary terrestrial vertebrate exists as an obligate scavenger but most if not all are facultative to some extent (Beasley et al. 2015). Therefore, we can use hyenas 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). The order Carnivora saw its origins in the Middle Eocene (56-33.9 Mya) where it split into the Caniforma and Feliforma. So we can trace efficient terrestrial movement by carnivores from this point on.

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

Of course, tetrapod terrestrial dominance predates the evolution of the dinosaurs. It is in the Permian, almost 300 millions years ago, that we have the earliest evidence of vertebrate scavenging where a temnospondyl amphibian fed on the carcass of *Varanops*, a predatory synapsid of the time (Reisz and Tsuji 2006). And it is with the evolution of endothermy in

1 the therapsid-mammal lineage (Clarke and Pörtner 2010) that terrestrial vertebrates would
2 have had the ability to range widely, a vital component in seeking out carrion.

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

10 Flight is a cheaper means of locomotion than walking or running (Tucker 1975). Many
11 extant birds exist as facultative scavengers; storks, eagles, corvids, are all known to take
12 substantial quantities of carrion in their diet (Kendall 2013). The advantage of flight can be
13 extended further in larger species that engage in soaring instead of flapping flight, which is
14 even cheaper still (approximately twice the basal metabolic rate) (Hedenstrom 1993, Spivey
15 et al. 2014). The benefits this confers are clear from the information we have on the
16 enormous foraging ranges of many vultures (Spiegel et al. 2013) and seabirds (Thaxter et al.
17 2012). In the former case we have the best known scavengers on Earth. Vultures consist of
18 two convergent groups, from the old and the new world and represent the only example of
19 obligate vertebrate scavengers today. The families from which modern vultures arose, the
20 Accipitridae and Cathartidae, appear during the Palaeocene (66 - 56 Mya) (Jetz et al. 2012,
21 Jarvis et al. 2014). Avian flight is far older than this and originates in the Late Jurassic
22 (163.5-145 Million years ago - Mya), coincident with the fossils of *Archaeopteryx*
23 *lithographica* so many of these benefits would have been realised from that point on for
24 carnivorous birds. However, vertebrate flight is much older still where pterosaurs predate bird
25 origins by a considerable margin in the Late Triassic (235-201.3 Mya). Scavenging in this
26 diverse group has been hypothesised many times before (Witton and Naish 2008). Certain

1 clades of these animals could reach enormous sizes (e.g. Azhdarchids with wingspans of 11
2 metres (Witton and Habib 2010)) and, notably, look to have engaged in soaring flight
3 (Witton and Habib 2010).

4 The only other vertebrate group capable of powered flight are the bats where scavenging
5 has not been recorded to our knowledge. The bat fossil record is notoriously poor owing to
6 their fragile skeletons so we are unable to determine if extinct species were more suited to
7 this lifestyle (Eiting and Gunnell 2009). Although it does not seem that flight is the main
8 criterion precluding them from scavenging (see below).

9 Aquatic scavengers have a locomotory benefit because water is a medium that is
10 conducive to low-cost movement (Tucker 1975). In fact, the cost of swimming is lower than
11 either running or flying (Williams 1999). This has led some researchers to argue for the
12 feasibility of a scavenging fish (Ruxton and Houston 2004a, Ruxton and Bailey 2005). As
13 with the aerial and terrestrial environments we have evidence of facultative scavenging among
14 extant and extinct aquatic species. For example, the remains of a mosasaur and a terrestrial
15 hadrosaur were discovered with embedded teeth from a Cretaceous shark, *Squalicorax*
16 (Schwimmer et al. 1997). As well as a likely instance of scavenging between a
17 4-million-year-old white shark (*Carcharodon*) and mysticete whale from Peru (Ehret et al.
18 2009). We might expect then that by combining an aquatic environment and an endothermic
19 metabolism that marine mammals would prosper as scavengers. We know fossil pinnipeds
20 and cetaceans from 60 Mya have transitional features indicative of their trajectory to fully
21 aquatic species (Williams 1999). But despite this movement away from land the energetic
22 savings were negligible because the *total* cost incurred by a swimming marine mammal is
23 high (Williams 1999). As Williams (1999) notes, "Free-ranging animals must contend with
24 the total energetic expenditure associated with supporting basic biological functions as well as
25 with moving the body and appendages through the environment."

Detection

A simplification of terrestrial, vertebrate scavengers in sensory terms is one of them existing in a two-dimensional plane while foraging for carrion directly. They can detect carcasses at a range that is defined by the radius of their sensory organs. As a consequence, they have a much more restricted view of the landscape than do aerial foragers. Hyenas have well developed sensory organs, whereby they can smell a rotting carcass 4 km away and can hear the vocalisations of conspecifics at a distance of 10 km (Mills 1989). Using the approach of Spiegel et al. (2013) we estimate a spotted hyena could resolve a 2 metre target at 1 km distance. Ruxton and Houston (2004b) calculated that "a 1 tonne mammal or reptile, in an ecosystem yielding carrion at densities similar to the current Serengeti, could have met its energy requirements if it could detect carrion over a distance of the order of 400–500 m."

Species capable of flight have effectively added an extra spatial dimension, i.e. the vertical component, to their sensory environment over land animals. This allows them to look down on a landscape where they are unencumbered by obstacles that would obstruct the view of a terrestrial scavenger. Such an ability has obvious benefits in detecting carrion. Vultures are known to have impressive visual acuity with one estimate indicating Lappet-faced Vultures (*Torgos tracheliotus*) are capable of detecting a 2 metre carcass over 10 km away (Spiegel et al. 2013). Eagles too are known to have highly developed visual abilities (Reymond 1985). It follows from this that the evolution of flight allowed aerial animals to detect far more carrion than their terrestrial counterparts (Lisney et al. 2013).

Moreover, having a panoramic view means being able to gather a wealth of information from other foragers, be they conspecifics or other species (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 forage far more efficiently because one bird can scrounge information on the location of food from another successful forager (Kane et al. 2014).

1 Aside from sight, three species within the new world family Cathartidae, (genus
2 *Cathartes*), have well developed olfactory systems (Lisney et al. 2013). Among them are the
3 Turkey Vultures (*Cathartes aura*) which were able to locate 90% of baits set out in a tropical
4 forest (Houston 1986). An atuned sense of smell is obviously useful in detecting decaying
5 carrion. Clearly, it would be pointless to have incredible ranging abilites and not have the
6 sensory architecture to benefit from it.

7 Returning to bats, their visual acuity is famously poor, and echolocation would not lend
8 itself to discovering immobile carrion. Their small size and poor terrestrial ability would also
9 count against them at a carcass (Riskin et al. 2006).

10 Depending on the species, a carcass in water either floats or descends to the sea floor
11 (Whitehead and Reeves 2005). In the latter low-light environment, visual detection distances
12 are far lower (< 100 m) than they would be in the air. As such, animals detect resources
13 through chemo- and mechanoreception more so than through vision (Ruxton and Houston
14 2004a). Extant aquatic snakes are deemed as having the most suitable physiology for
15 scavenging. A hypothesis put forth by Sazima and Strüssmann (1990) argued that chemical
16 gradients in water would allow for a relatively easier detection of carrion. This gained some
17 support from DeVault and Krochmal (2002), who found a preponderence of aquatic snake
18 species in their review of this behaviour.

19 **Processing**

20 Since carrion is not dispatched directly, often the most easily accessible and choicest
21 components of the carcass will be missing or, if present, will be fought over. Being able to
22 extract nutrients from remnants gives the scavenger a great advantage. Thus, the bone
23 crushing ability of hyenas reveals another useful scavenger trait. Osteophagy is known across
24 a range of terrestrial carnivores and given some fat-rich mammalian bones have an energy
25 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 110 kg *Pachycrocuta brevirostris* during the Pliocene (Palmqvist et al. 2011). Some work on extinct sabretooths suggests they may have left a large amount of food for would-be scavengers because of their unique skull morphology. As a result, the decline of Machairodontinae sabretooths has been offered as an explanation for the extinction of *P. brevirostris* (Palmqvist et al. 2011). The bone-crushing dogs that evolved during the Oligocene (subfamily Borophaginae) have been compared to hyenas in terms of their feeding ecology as well (Van Valkenburgh et al. 2003, Martín-Serra et al. 2016). Certainly, it is profitable to compare extant terrestrial species to their prehistoric forebears given the dominance of mammalian carnivores since the Eocene.

Interestingly, such comparisons have given insight into the feeding ecology of early hominins who, for instance, had the ability to craft tools for breaking open bones (Blasco et al. 2014). The question of where our ancestors placed on the hunter-scavenger axis during the Plio-Pleistocene has been a matter of debate for years. A recent study investigating potential scavenging opportunities for hominins in Kenya found that, even when discounting bone 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. 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 intelligence, resultant tool-use and cooperative nature of hominins meant they could likely adapt to take on more or less carrion depending on their environment (Moleón et al. 2014).

When it comes to reptiles they possess an advantage here, in that over the course of a year their food requirements can be 30 times smaller than an endotherm of equal size (Nagy 2005). Any adaptations that reduce energetic costs are likely to be selected in scavengers.

DeVault and Krochmal (2002) suggest this is an avenue for scavenging in snakes because they “exhibit exceedingly low maintenance metabolisms, and most can survive on a few scant feedings per year. It is, therefore, possible for snakes to rely largely on infrequent, less energy-rich meals.” In the same review the authors found occurrences of scavenging spread across five families of snakes and stated that this behaviour is “far more common than currently acknowledged.”(DeVault and Krochmal 2002). The same reasoning can be applied to crocodiles and their allies (Forrest 2003). A sit and wait strategy is viable for an ectotherm.

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

In Mesozoic systems some extremely large theropod dinosaurs had a morphology which suggests an ability to process bone e.g. the robust skull and dentition of *T. rex* (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). This is noted as being powerful enough to break open skeletal material (Rayfield et al. 2001).

1 Scavenging should be particularly attractive to avian predators compared to mammals.
2 Solitary mammalian predators can kill prey up to the same body mass as themselves and
3 sometimes an order of magnitude heavier (e.g. socially hunting lions (Owen-Smith and Mills
4 2008)). In contrast, birds of prey tend to kill prey smaller than themselves (Slagsvold and
5 A Sonerud 2007). This is likely due to their need to kill prey that they can fly away with, as
6 well as the risk of injury being higher (which carries a higher mortality risk) for a bird than a
7 mammal. Thus for birds, scavenging means they can exploit species that would otherwise be
8 too big for them to kill.

9 Large body size confers substantial dominance and starvation-resistance benefits (Ruxton
10 and Houston 2004b). Thus, we would expect scavengers to have this trait selected for even
11 in the case of weight-constrained fliers. Cinereous Vultures (*Aegypius monachus*) and condors
12 (*Vultur gryphus*, *Gymnogyps californianus*) all have body masses that can exceed 10 kg and
13 represent some of the heaviest bird species capable of flight (Ferguson-Lees and Christie
14 2001, Donázar et al. 2002).

15 And as we have noted the Azhdarchid pterosaurs were far bigger again, with estimated
16 body masses of over 200 kg (Witton and Habib 2010). Although Witton and Naish (2008)
17 argued that neck inflexibility and straight, rather than hooked jaw morphology points against
18 pterosaurs existing as *obligate* scavengers, Azhdarchid terrestrial proficiency indicates they
19 would have been comfortable foraging on the ground. Indeed, extant Marabou Storks
20 (*Leptoptilos crumenifer*) have a comparable morphology and are noted facultative scavengers
21 so it is reasonable to believe that certain pterosaurs behaved similarly.

22 The competitive ability of even the largest bird is radically diminished in their interactions
23 with mammalian competitors however, and as such they tend to consume carrion rapidly.
24 Houston (1974) observed a group of *Gyps* vultures consuming all of the soft tissue from a 50
25 kg Grant's gazelle *Nanger granti* in eight minutes.

26 The first bird lineages did not have beaks and were predominantly carnivorous (Martyniuk

2012). This implies that, among the earliest species, scavenging would have been a live opportunity cf. their descendants who evolved beaks, restricting their ability to consume flesh.

Avian scavengers have to compete with microorganisms and so 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* had an average pH of 1.5, which enables them to consume fisheries discards.

Big bats (which are better suited for scavenging, following our previous argument) are typically frugivores and therefore probably lack of adaptations for digesting meat. While carnivorous bats are mainly found in the microbats which are insectivorous.

Environment

Both the biotic and abiotic environment a would-be scavenger finds itself in can influence to degree to which it can depend on carrion. As noted earlier, a system similar to the Serengeti in productivity could have supported a terrestrial scavenger (Ruxton and Houston 2004b). 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 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. The absence of flying vertebrates in the Palaeozoic may have permitted terrestrial forms to take in a higher proportion of carrion in their diet. Osteophagy may have been even more viable during the Mesozoic era because the body mass distribution of herbivores tended to be skewed towards larger sizes (O’Gorman and Hone 2012). When we couple this with the fact that skeletal

1 mass scales greater than linearly with body mass (Prange et al. 1979) there would have been
2 a lot of bone material to consume in the environment provided an animal had the biology to
3 process it (Chure and Fiorillo 1997). As we discussed earlier, osteophagy could be extremely
4 beneficial to a scavenger.

5 Vultures and eagles tend to soar using thermals and if these air pockets don't form, say
6 on a cloudy day, the bird is grounded (Mundy et al. 1992). In many habitats (e.g. the arctic)
7 it is simply not possible for sufficiently powerful thermals to form and as a consequence
8 large-bodied vultures cannot exist. The upshot of this is that terrestrial carnivores like bears
9 and wolves take more carrion (DeVault et al. 2003). The use of different sensory systems also
10 illustrates the impact of the environment. The relatively open savanna systems of Africa are
11 well suited to a visually dependent vulture whereas more forested areas would select for
12 species that have a well developed olfactory system (Houston 1986).

13 A major difficulty for terrestrial scavengers is competition with vultures. Nocturnal
14 behaviour in the Hyaenidae in general has been put forth as an adaptation to reduce
15 competition with these exclusively diurnal birds (Gittleman 2013).

16 The presence of occasional bounties of carrion in the form of whale falls has led some
17 researchers to investigate if a scavenger could survive by seeking out these remains
18 exclusively. Ruxton and Bailey (2005) argued that although this is energetically feasible it's
19 ecologically unlikely. Any animal that could seek out such whale carcasses is unlikely to have
20 ignored other types of carrion. Although no aquatic species have ever exceeded the size of
21 whales, some enormous animals have evolved in this environment before the evolution of
22 whales, including *Leedsichthys*, a bony fish from the Middle Jurassic (174.1-163.5 Mya), that
23 weighed in excess of 20 tonnes. Thus, the energetic feasibility of a marine scavenger has a
24 long history. One point of interest is that of the whaling industry, which provided a bonanza
25 of floating carcasses especially during the 20th century (Whitehead and Reeves 2005). This
26 meant Killer Whales (*Orcinus orca*) could switch from hunting to scavenging, a switch made

1 that much easier by the noise of the whaling vessels that would effectively ring the
2 "dinner-bells" (Whitehead and Reeves 2005). Early whales such as *Basilosaurus* seem to fit
3 into the same niche as Killer Whales and we have some evidence for scavenging in this group
4 as well (Fahlke 2012).

5 **Conclusion**

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

19 **Acknowledgments**

20 A lot of people are to thank here.

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