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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. 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 carrion processing and a carrion producing environment.

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.

1 The Difficulty of Scavenging

2 The chief hurdle to scavenging is finding a sufficient quantity of food, the occurrence of which
3 is difficult to predict in space and time. Thus, any animal existing as a scavenger must
4 minimise its locomotory costs and maximise its detection capabilities (Ruxton and Houston
5 2004b). Once found, the scavenger has to process the carrion and overcome the agents of
6 decay produced by the action of microorganisms on the carcass (Ruxton et al. 2014). The
7 habitat must also be productive enough to sustain an animal biomass that will eventually
8 produce carcasses. We can draw on the image of a scavenger moving through its
9 environment, searching for food and trying to process it efficiently as we explore the
10 prevalence of this behaviour through time.

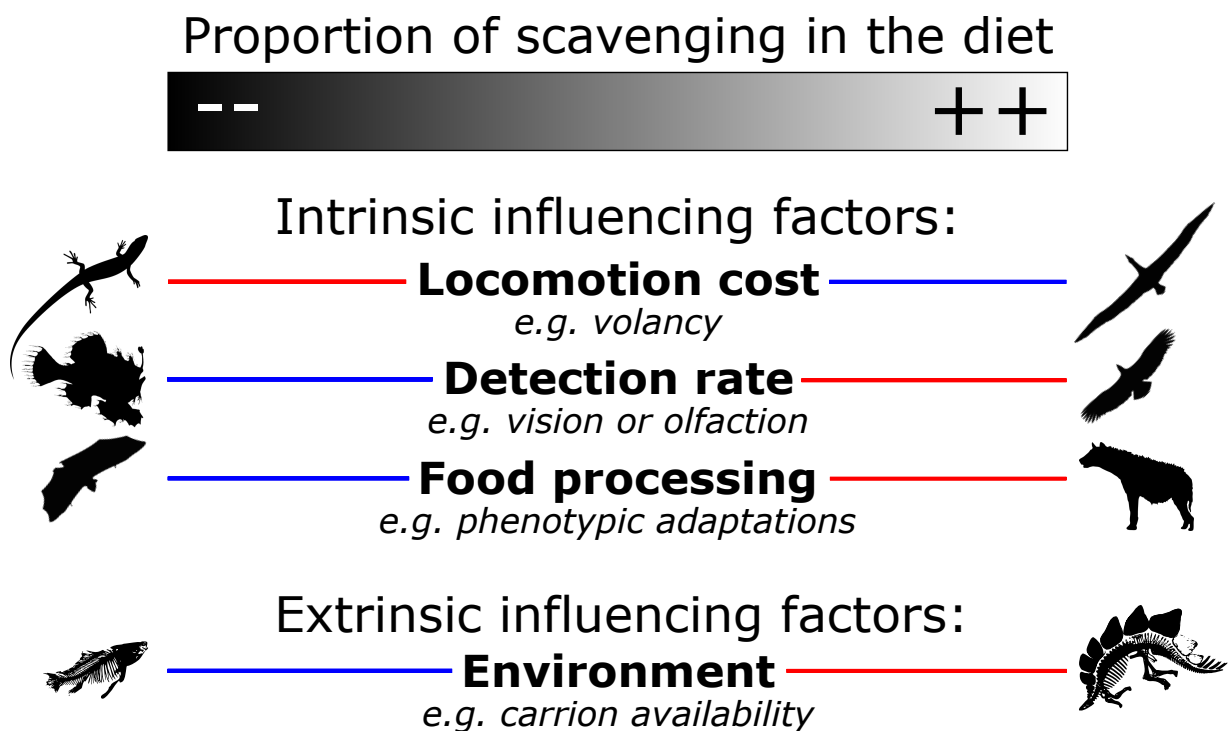


Figure 1: Factors influencing the proportion of scavenging in a vertebrates' diet. Blue lines indicates a reduction in the factor and red lines indicates an increase.

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). This constraint 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 $1.15 \times \text{body mass (kg)}^{0.12}$ and $0.23 \times \text{body mass (kg)}^{0.12}$ respectively (Ruxton and Houston 2004b). We can insert these into a foraging radius model $\frac{\text{duration} \times \text{speed}}{2} / 1000$ 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). For a foraging scavenger, this ability translates into a greater area searched for food.

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). And although no contemporary terrestrial vertebrate exists as an obligate scavenger most if not all are facultative to some extent (Beasley et al. 2015). The particular reliance of hyenas on carrion means we can use them as examples of efficient terrestrial scavengers to compare with other forms. In terms of locomotion, they employ a characteristic "rocking horse gait" which allows them to cover great distances efficiently, loping at 10 km/hr (Mills 1989, Jones et al. 2015). Such long-distance travel is apparent in African wild dogs (*Lycaon pictus*) and many other canids (Pennycuick 1995, Janis and Figueirido 2014). In contrast, big cats like leopards (*Panthera pardus*) rely on ambush (Pennycuick 1995). This allows us to make a broad distinction

1 between the ambush strategies of cats and the pursuit/ pounce strategies of dogs, the latter
2 being more suited to scavenging (Janis and Figueirido 2014). We can (and have) use(d)
3 these insights to compare extant terrestrial species to their prehistoric forebears given the
4 dominance of mammalian carnivores since the Eocene 56-33.9 Million years ago (Mya) where
5 the order split into the Caniforma and Feliforma (Van Valkenburgh 1987). To take one
6 example, Anyonge (1996) found *Nimravides*, a genus of sabretooth cat from the Miocene
7 (10.3 to 5.3 M ya) were likely to have been ambush predators which would have counted
8 against them taking a lot of carrion.

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

21 Of course, tetrapod terrestrial dominance predates the evolution of the dinosaurs. It is
22 during the Permian (298.9 - 252.17 Mya) that we have the earliest evidence of vertebrate
23 scavenging where a temnospondyl amphibian fed on the carcass of *Varanops*, a predatory
24 synapsid of the time (Reisz and Tsuji 2006). And it is with the evolution of endothermy in
25 the therapsid-mammal lineage (Clarke and Pörtner 2010) that terrestrial vertebrates would
26 have gained the ability to range widely, a vital component in seeking out carrion.

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

8 But it is in the air that we find scavengers par excellence. Flight is a cheaper means of
9 locomotion than walking or running (Tucker 1975). We know that many extant birds exist as
10 facultative scavengers because storks, raptors and corvids all take substantial quantities of
11 carrion in their diet (Kendall 2013). The advantage of flight can be extended further in larger
12 species that engage in soaring instead of flapping flight, which is even cheaper still
13 (approximately twice the basal metabolic rate) (Hedenstrom 1993, Spivey et al. 2014). The
14 benefits this confers are clear from the information we have on the enormous foraging ranges
15 of many vultures (Spiegel et al. 2013) and seabirds (Thaxter et al. 2012). In vultures we have
16 the best known scavengers on Earth. These birds consist of two convergent groups, from the
17 old and the new world where they represent the only example of obligate vertebrate
18 scavengers today. The families from which modern vultures arose, the Accipitridae and
19 Cathartidae, appear during the Palaeocene (66 - 56 Mya; Jetz et al. 2012, Jarvis et al.
20 2014). Yet, avian flight is far older than this and originates in the Late Jurassic (163.5-145
21 Mya), coincident with the fossils of *Archaeopteryx lithographica* so many of these benefits
22 would have been realised from that point on for carnivorous birds. And vertebrate flight is
23 much older still where pterosaurs predate bird origins by a considerable margin in the Late
24 Triassic (235-201.3 Mya). Scavenging in this diverse group has been hypothesised many times
25 before (Witton and Naish 2008). Certain clades of these animals could reach enormous sizes
26 (e.g. Azhdarchids with wingspans of 11 metres; Witton and Habib 2010) and, notably, look

1 to have engaged in soaring flight (Witton and Habib 2010).

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

7 Aquatic scavengers have a locomotory benefit because water is a medium that is
8 conducive to low-cost movement (Tucker 1975). In fact, the cost of swimming is lower than
9 either running or flying (Williams 1999). This has led some researchers to argue for the
10 feasibility of a scavenging fish (Ruxton and Houston 2004a, Ruxton and Bailey 2005). As
11 with the aerial and terrestrial environments we have evidence of facultative scavenging among
12 extinct aquatic species. For example, the remains of a mosasaur and a terrestrial hadrosaur
13 were discovered with embedded teeth from a Cretaceous shark, *Squalicorax* (Schwimmer
14 et al. 1997). As well as a likely instance of scavenging between a 4-million-year-old white
15 shark (*Carcharodon*) and mysticete whale from Peru (Ehret et al. 2009). Extant White sharks
16 *Carcharodon carcharias* too are known to feed on whale carcasses (Fallows et al. 2013). We
17 might expect then that by combining an aquatic environment and an endothermic
18 metabolism that marine mammals would prosper as scavengers. We know fossil pinnipeds
19 and cetaceans from 60 Mya have transitional features indicative of their trajectory to fully
20 aquatic species (Williams 1999). But despite this movement away from land the energetic
21 savings were negligible because the *total* cost incurred by a swimming marine mammal is
22 high (Williams 1999). This is not to say that aquatic mammalian scavengers don't exist, only
23 that their total energetic cost is similar to an equivalent terrestrial mammal.

Detection

It would be pointless to have incredible ranging abilities and not have the sensory architecture to benefit from it. If we came at this from a position of complete ignorance we would predict scavengers to have well-developed senses and indeed this is what we find. 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 make up for this in their ability to smell a rotting carcass 4 km away and to hear the vocalisations of conspecifics at a distance of 10 km (Mills 1989). While considering prehistoric habitats 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". The senses of many extant (and in all probability extinct) carnivores meet this required distance, making scavenging feasible for terrestrial species (Farlow 1994, Mech and Boitani 2010).

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,

1 returning to vultures, the genus *Gyps* consists of highly social and colonially nesting species
2 (Fernández-Bellon et al. 2015). These behaviours allow them forage far more efficiently
3 because one bird can scrounge information on the location of food from another successful
4 forager (Kane et al. 2014).

5 We can contrast this ability to bats, whose visual acuity is famously poor. It also appears
6 that echolocation would not lend itself to discovering immobile carrion. Their small size and
7 poor terrestrial ability would also count against them at a carcass (Riskin et al. 2006).

8 Aside from sight, three species of vultures within the new world family Cathartidae,
9 (genus *Cathartes*), have well developed olfactory systems (Lisney et al. 2013). Among them
10 are the Turkey Vultures (*Cathartes aura*) which were able to locate 90% of baits set out in a
11 tropical forest (Houston 1986). An atuned sense of smell is obviously useful in detecting
12 decaying carrion from the air.

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

Processing

Since carrion is not dispatched directly, often the most easily accessible and choicest components of the carcass will be missing or, if present, will be fought over. Being able to extract nutrients from remnants gives a scavenger a great advantage. Thus, the bone crushing ability of hyenas reveals another useful scavenger trait. Osteophagy is known across a range of terrestrial carnivores and given some fat-rich mammalian bones have an energy density (6.7 kJ/g) comparable with that of muscle tissue, it makes skeletal remains an enticing resource (Brown 1989). This ability reached its zenith among hyenas with the evolution of the 110 kg *Pachycrocuta brevirostris* during the Pliocene (3.6 - 2.58 Mya; 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; 33.9 - 23.03 Mya) have been compared to hyenas in terms of their feeding ecology as well (Van Valkenburgh et al. 2003, Martín-Serra et al. 2016).

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

1 intelligence, resultant tool-use and cooperative nature of hominins meant they could likely
2 adapt to take on more or less carrion depending on their environment (Moleón et al. 2014).

3 In Mesozoic systems some extremely large theropod dinosaurs had a morphology
4 indicative of an ability to process bone e.g. the robust skull and dentition of *T. rex* (Hone
5 and Rauhut 2010). There is direct evidence that *T. rex* did this in the form of distinctive
6 wear marks on its tooth apices (Farlow and Brinkman 1994, Schubert and Ungar 2005) and
7 the presence of bone fragments in its coprolites (Chin et al. 1998). The animal also had an
8 enormous bite force, with one estimate putting it at 57000 Newtons (Bates and Falkingham
9 2012). This is noted as being powerful enough to break open skeletal material (Rayfield et al.
10 2001).

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

21 In addition to reducing locomotory costs we would expect adaptations that reduce
22 energetic costs of maintenance to be selected for in scavengers because it would maximise
23 the benefit derived from such a sporadic food source. Extant reptiles possess an advantage
24 here, in that over the course of a year their food requirements can be 30 times smaller than
25 an endotherm of equal size (Nagy 2005). DeVault and Krochmal (2002) suggest this is an
26 avenue for scavenging in snakes because they "exhibit exceedingly low maintenance

1 metabolisms, and most can survive on a few scant feedings per year. It is, therefore, possible
2 for snakes to rely largely on infrequent, less energy-rich meals." In the same review the
3 authors found occurrences of scavenging spread across five families of snakes and stated that
4 this behaviour is "far more common than currently acknowledged." (DeVault and Krochmal
5 2002). The same reasoning can be applied to crocodiles and their allies (Forrest 2003). A sit
6 and wait strategy is viable for an ectotherm. This low existence cost is also realised in many
7 sharks who have coupled low locomotory costs with an ectothermic metabolism. The upshot
8 is that 30 kg of blubber can sustain a White shark for over six weeks (Carey et al. 1982).

9 Scavenging should be particularly attractive to avian predators compared to mammals.
10 Solitary mammalian predators can kill prey up to the same body mass as themselves and
11 sometimes an order of magnitude heavier (e.g. socially hunting lions (Owen-Smith and Mills
12 2008)). In contrast, birds of prey tend to kill prey smaller than themselves (Slagsvold and
13 A Sonerud 2007). This is likely due to their need to kill animals that they can fly away with,
14 as well as the risk of injury being higher (which carries a higher mortality risk) for a bird than
15 a mammal. Scavenging provides a means for birds to exploit species that would otherwise be
16 too big for them to kill.

17 Large body size confers substantial dominance and starvation-resistance benefits (Ruxton
18 and Houston 2004b). Thus, we would expect scavengers to have this trait selected for even
19 in the case of weight-constrained fliers. Cinereous Vultures (*Aegypius monachus*) and condors
20 (*Vultur gryphus*, *Gymnogyps californianus*) all have body masses that can exceed 10 kg and
21 represent some of the heaviest bird species capable of flight (Ferguson-Lees and Christie
22 2001, Donazar et al. 2002).

23 And as we have noted the Azhdarchid pterosaurs were far bigger again, with estimated
24 body masses of over 200 kg (Witton and Habib 2010). Although Witton and Naish (2008)
25 argued that neck inflexibility and straight, rather than hooked jaw morphology points against
26 pterosaurs existing as *obligate* scavengers, Azhdarchid terrestrial proficiency indicates they

1 would have been comfortable foraging on the ground. Indeed, extant Marabou Storks
2 (*Leptoptilos crumenifer*) have a comparable morphology and are noted facultative scavengers
3 so it is reasonable to believe that certain pterosaurs behaved similarly.

4 The competitive ability of even the largest bird is radically diminished in their interactions
5 with mammalian competitors however, and as such they tend to consume carrion rapidly.
6 Houston (1974) observed a group of *Gyps* vultures consuming all of the soft tissue from a 50
7 kg Grant's gazelle (*Nanger granti*) in eight minutes. Their serrated tongues and hooked bills
8 enabling them to achieve this feat (Houston and Cooper 1975). Outside of raptors like
9 vultures the specialised beaks of many modern bird lineages hinders their ability to eat meat.
10 Martyniuk (2012) notes that the first bird lineages did not have beaks and were
11 predominantly carnivorous. This implies that, among the earliest species, scavenging would
12 have been a live opportunity cf. their descendants.

13 Shviki (2006) points out that "evolutionary pressures favor detection maximizers relative
14 to toxification minimizers in competitive interactions for carcasses." But the fact remains that
15 overcoming microorganism toxins is still a beneficial adaptation to any scavenger. Avian
16 scavengers have evolved incredibly acidic stomachs that allow them to consume and process
17 putrefied flesh with no ill effects (Houston and Cooper 1975, Roggenbuck et al. 2014). This
18 adaptation is not restricted to vultures though, Grémillet et al. (2012) showed wandering
19 albatrosses (*Diomedea exulans* so-called 'vultures of the seas') had an average pH of 1.5,
20 which enables them to consume fisheries discards. Outside of the birds there is evidence of
21 selection for 'toxification minimizers'. From our earlier arguments we know that ectotherms
22 are limited in their ability to find carrion as quickly as endotherms. This implies later arrivers
23 would benefit especially from well-developed detoxifying apparatus. Shviki (2006) suggests
24 that "specialized oral structures in snakes may have evolved under pressures associated with
25 scavenging." Moreover, some authorities have charted an evolutionary course from basal
26 fossorial snakes to modern terrestrial species by way of an obligate scavenger intermediate

(Bauchot 2006).

It is in the ability to process carrion that bats suffer. Big bats (which are better suited for scavenging, following our previous argument) are typically frugivores and therefore lack the 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 we noted before, 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. Osteophagy may have been even more viable during the Mesozoic era 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). As we discussed earlier, this ability is often extremely beneficial to a scavenger.

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. The upshot of this is that terrestrial carnivores like bears

1 and wolves take more carrion (DeVault et al. 2003). Certainly, a major difficulty for terrestrial
2 scavengers is competition with vultures. Nocturnal behaviour in the hyaenidae in general has
3 been put forth as an adaptation to reduce competition with these exclusively diurnal birds
4 (Gittleman 2013). If we apply this line of reasoning over evolutionary time-scales, the absence
5 of flying vertebrates in the Palaeozoic may have permitted terrestrial forms to take in a
6 higher proportion of carrion in their diet.

7 The use of different sensory systems also illustrates the impact of the environment. The
8 relatively open savanna systems of Africa are well suited to a visually dependent vulture
9 whereas more forested areas would select for species that have a well-developed olfactory
10 system (Houston 1986). Again, a similar line of reasoning can be applied to aquatic species
11 depending whether they forage near the well-lit surface or the dark benthos.

12 Staying in the aquatic setting, the phenomenon of occasional bounties of carrion in the
13 form of whale falls has led some researchers to investigate if a scavenger could survive by
14 seeking out these remains exclusively. Ruxton and Bailey (2005) argued that although this is
15 energetically feasible it's ecologically unlikely. Any animal that could find such whale
16 carcasses is unlikely to have ignored other types of carrion. Although no aquatic species have
17 ever exceeded the size of whales, some enormous animals have evolved in this environment
18 before the evolution of whales, including *Leedsichthys*, a bony fish from the Middle Jurassic
19 (174.1-163.5 Mya), that weighed in excess of 20 tonnes. Thus, the energetic feasibility of a
20 marine scavenger that specialises on large carcasses has a long history. One point of interest
21 is that of the whaling industry, which provided a bonanza of floating carcasses especially
22 during the 20th century (Whitehead and Reeves 2005). This meant Killer Whales (*Orcinus*
23 *orca*) could switch from hunting to scavenging, a switch made that much easier by the noise
24 of the whaling vessels that would effectively ring the "dinner-bells" (Whitehead and Reeves
25 2005). Early whales such as *Basilosaurus* seem to fit into the same niche as Killer Whales
26 and we have some evidence for scavenging in this group as well (Fahlke 2012).

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

Conclusion

As is often the case in science, the present provides the key to the past. The animals of today, while often different (sometimes radically so) to their ancestors, allow us to make informed comparisons to extinct species. We have used this technique to give insight into the drivers of scavenging across terrestrial vertebrates through time. In common with any other forager be they grazer, browser or predator, scavengers past and present have had to balance their energetic costs with the gains of food.

¹ **Acknowledgments**

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