

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.

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 in order to take in a sufficient
7 amount of energy (Ruxton et al. 2014). The habitat must also be productive enough to
8 sustain an animal biomass that will eventually produce carcasses. We can draw on the image
9 of a scavenger moving through its environment, searching for food and trying to process it
10 efficiently as we explore the prevalence of this behaviour through time.

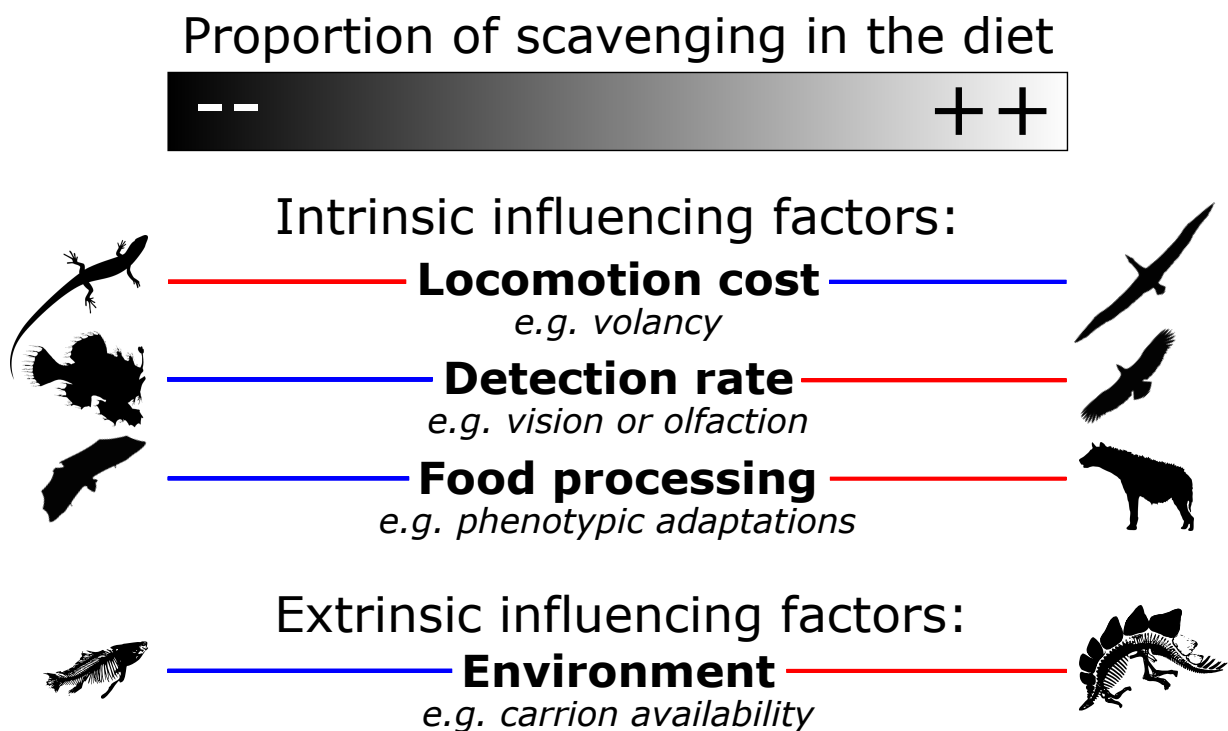


Figure 1: Factors influencing the proportion of scavenging in a vertebrates' diet. Blue lines indicates a reduction in the factor and red lines indicates an increase.

1 Locomotion

2 As endotherms, mammals can sustain long bouts of energetically expensive activity. By
3 contrast, modern reptiles are ectothermic, limiting their activity periods. This is exacerbated
4 by the sprawling gait seen in many lizards which results in Carrier's Constraint such that the
5 animal can't move and breathe at the same time because the lateral movements impede its
6 lungs (Carrier 1987). These constraints manifest themselves in aspects such as maximum
7 sustainable speed where an equivalent mammal has a six to seven fold increase (Ruben
8 1995). To quantify this effect with a simple example we can turn to some allometric
9 relationships relating sustainable travelling speed to body mass. In the case of mammals and
10 reptiles these are $1.15 \times \text{body mass (kg)}^{0.12}$ and $0.23 \times \text{body mass (kg)}^{0.12}$ respectively
11 (Ruxton and Houston 2004b). If we insert these into a foraging radius model $\frac{\text{duration} \times \text{speed}}{2} / 1000$
12 for a 12 hour foraging day which shows that while a 10 kg reptile can range 6.5 km an
13 equally sized mammal can range nearly 33 km (Enstipp et al. 2006). For a foraging
14 scavenger, this ability translates into a greater area searched for food.

15 Today, terrestrial scavenging in the mammals is probably best known in an African
16 context where hyenas, jackals and lions all take sizable proportions of carrion in their diet. In
17 the spotted hyena (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*) and brown hyena
18 (*Hyaena brunnea*) it can be over 90% (Jones et al. 2015). And although no contemporary
19 terrestrial vertebrate exists as an obligate scavenger most (if not all) are facultative to some
20 extent (Beasley et al. 2015). The particular reliance of hyenas on carrion means we can use
21 them as examples of efficient terrestrial scavengers to compare with other forms. In terms of
22 locomotion, they employ a characteristic "rocking horse gait" which allows them to cover
23 great distances efficiently, loping at 10 km/hr (Mills 1989, Jones et al. 2015). Such
24 long-distance travel is apparent in African wild dogs (*Lycaon pictus*) and many other canids
25 (Pennycuik 1995, Janis and Figueirido 2014). In contrast, big cats like leopards (*Panthera*
26 *pardus*) rely on ambush (Pennycuik 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 that *Nimravides*, a genus of sabretooth cat from the
7 Miocene (10.3 to 5.3 Mya) were likely to have been ambush predators which would have
8 counted 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, the importance of terrestrial tetrapods predates the evolution of the dinosaurs.
22 It is during the Permian (298.9 - 252.17 Mya) that we have the earliest evidence of
23 vertebrate scavenging where a temnospondyl amphibian fed on the carcass of *Varanops*, a
24 predatory synapsid of the time (Reisz and Tsuji 2006). And it is with the evolution of
25 endothermy in the therapsid-mammal lineage (Clarke and Pörtner 2010) that terrestrial
26 vertebrates would have gained the ability to range widely, a vital component in seeking out

1 carrion.

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

9 But it is in the air that we find scavengers *par excellence*. Flight is a cheaper means of
10 locomotion than either walking or running (Tucker 1975). We know that many extant birds
11 exist as facultative scavengers because storks, raptors and corvids all take substantial
12 quantities of carrion in their diet (Kendall 2013). The advantage of flight can be extended
13 further in larger species that engage in soaring instead of flapping flight, which is even
14 cheaper still (pproximately twice the basal metabolic rate; Hedenstrom 1993, Spivey et al.
15 2014). The benefits this confers are clear from the information we have on the enormous
16 foraging ranges of many vultures (Spiegel et al. 2013) and seabirds (Thaxter et al. 2012).
17 The difficulty inherent in observing marine birds foraging at sea means our knowledge of their
18 feeding habits is limited. But it does seem that albatrosses, who can range many 100s of
19 kilometres, take a substantial amount of carrion in their diet (Croxall and Prince 1994). This
20 is typically in the form of squid, which float on the surface, allowing the birds to readily pluck
21 their remains out of the water (Croxall and Prince 1994). In vultures, who are more easily
22 observed on land, we have the best known scavengers on Earth. These birds consist of two
23 convergent groups, from the old and the new world where they represent the only example of
24 obligate vertebrate scavengers to date.

25 The families from which modern vultures arose, the Accipitridae and Cathartidae, appear
26 during the Palaeocene (66 - 56 Mya; Jetz et al. 2012, Jarvis et al. 2014). Yet, avian flight is

1 far older than this and originates in the Late Jurassic (163.5-145 Mya), coincident with the
2 fossils of *Archaeopteryx lithographica*, so many of these benefits would have been realised
3 from that point on for carnivorous birds. And vertebrate flight is much older still where
4 pterosaurs predate bird origins by a considerable margin in the Late Triassic (235-201.3 Mya).
5 Scavenging in this diverse group has been hypothesised many times before (Witton and Naish
6 2008). Certain clades of these animals could reach enormous sizes (e.g. Azhdarchids with
7 wingspans of 11 metres; Witton and Habib 2010) and, notably, look to have engaged in
8 soaring flight (Witton and Habib 2010).

9 The only other vertebrate group capable of powered flight are the bats where scavenging
10 has not been recorded to our knowledge. However, some fossil evidence as early as in the
11 Eocene (56 to 33.9 Mya) suggest the presence of possible scavenging bats. A large bat from
12 the middle to late Eocene (56 to 33.9 Mya) with a robust cranio-mandibular morphology,
13 *Necromatis* ("death-eater"), could have intake carrion as a significant proportion of its diet
14 (Weithofer 1887, Hand et al. 2012). However, this example might be peculiar to this
15 exceptional fossil given most other fossils represent animals less suited to the lifestyle (Eiting
16 and Gunnell 2009).

17 Aquatic scavengers have a locomotory benefit because water is a medium that is
18 conducive to low-cost movement (Tucker 1975). In fact, the cost of swimming is lower than
19 either running or flying (Williams 1999). This has led some researchers to argue for the
20 feasibility of a scavenging fish (Ruxton and Houston 2004a, Ruxton and Bailey 2005). As
21 with the aerial and terrestrial environments we have evidence of facultative scavenging among
22 extinct aquatic species. For example, the remains of a mosasaur and a terrestrial hadrosaur
23 were discovered with embedded teeth from a Cretaceous shark, *Squalicorax* (Schwimmer
24 et al. 1997). As well as a likely instance of scavenging between a 4-million-year-old white
25 shark (*Carcharodon*) and mysticete whale from Peru (Ehret et al. 2009). Extant White sharks
26 *Carcharodon carcharias* too are known to feed on whale carcasses (Fallows et al. 2013). We

1 might expect then that by combining an aquatic environment and an endothermic
2 metabolism that marine mammals would prosper as scavengers. We know fossil pinnipeds
3 and cetaceans from 60 Mya have transitional features indicative of their trajectory to fully
4 aquatic species (Williams 1999). But despite this movement away from land the energetic
5 savings were negligible because the *total* cost incurred by a swimming marine mammal is
6 high (Williams 1999). This is not to say that aquatic mammalian scavengers don't exist, only
7 that their total energetic cost is similar to an equivalent terrestrial mammal.

8 **Detection**

9 It would be pointless to have incredible ranging abilities and not have the sensory architecture
10 to benefit from it. If we came at this from a position of complete ignorance we would predict
11 scavengers to have well-developed senses and indeed, this is what we find. A simplification of
12 terrestrial, vertebrate scavengers in sensory terms is one of them existing in a two-dimensional
13 plane while foraging for carrion directly. They can detect carcasses at a range that is defined
14 by the radius of their sensory organs. As a consequence, they have a much more restricted
15 view of the landscape than do aerial foragers. Hyenas make up for this in their ability to
16 smell a rotting carcass 4 km away and to hear the vocalisations of conspecifics at a distance
17 of 10 km (Mills 1989). While considering prehistoric habitats Ruxton and Houston (2004b)
18 calculated that "a 1 tonne mammal or reptile, in an ecosystem yielding carrion at densities
19 similar to the current Serengeti, could have met its energy requirements if it could detect
20 carrion over a distance of the order of 400–500 m". The senses of many extant (and in all
21 probability extinct) carnivores meet this required distance, making scavenging feasible for
22 terrestrial species (Farlow 1994, Mech and Boitani 2010).

23 Species capable of flight have effectively added an extra spatial dimension, i.e. the
24 vertical component, to their sensory environment over land animals. This allows them to look
25 down on a landscape where they are unencumbered by obstacles that would obstruct the view

1 of a terrestrial scavenger. Such an ability has obvious benefits in detecting carrion. Vultures
2 are known to have impressive visual acuity, with one estimate indicating Lappet-faced
3 Vultures (*Torgos tracheliotus*) are capable of detecting a 2 metre carcass over 10 km away
4 (Spiegel et al. 2013). Eagles too are known to have highly developed visual abilities
5 (Reymond 1985). It follows from this that the evolution of flight allowed aerial animals to
6 detect far more carrion than their terrestrial counterparts (Lisney et al. 2013).

7 Moreover, having a panoramic view means being able to gather a wealth of information
8 from other foragers, be they conspecifics or other species (Jackson et al. 2008). Again,
9 returning to vultures, the genus *Gyps* consists of highly social and colonially nesting species
10 (Fernández-Bellon et al. 2015). These behaviours allow them forage far more efficiently
11 because one bird can scrounge information on the location of food from another successful
12 forager (Kane et al. 2014).

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

16 Aside from sight, many birds have well developed olfactory systems (Lisney et al. 2013)
17 including three species of vultures within the new world family Cathartidae, (genus
18 *Cathartes*). Among them are the Turkey Vultures (*Cathartes aura*) which were able to locate
19 90% of baits set out in a tropical forest (Houston 1986). An attuned sense of smell is
20 obviously useful in detecting decaying carrion from the air.

21 Aquatic species have to contend with the low-light environment of water where visual
22 detection distances are far lower (< 100 m) than they would be in the air. As such, animals
23 here detect resources through chemo- and mechanoreception more so than through vision
24 (Ruxton and Houston 2004a). This is particularly relevant to extant sharks and aquatic
25 snakes who are deemed as having the most suitable physiology for scavenging. A hypothesis
26 put forth by Sazima and Strüssmann (1990) argued that chemical gradients in water would

allow for a relatively easier detection of carrion by snakes. This gained some support from DeVault and Krochmal (2002), who found a preponderance of aquatic snake species in their review of this behaviour. Smell seems to be the primary means of carcass detection in sharks as well. Fallows et al. (2013) found that wind speed determined the number of sharks feeding at whale carcasses indicating they were dependent on detecting the odours from the decaying whales.

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

1 the Plio-Pleistocene has been a matter of debate for years. A recent study investigating
2 potential scavenging opportunities for hominins in Kenya found that, even when discounting
3 bone material, there is a substantial amount of scavengeable meat left on predated remains;
4 sufficient to sustain the requirements of an adult male *Homo erectus* (Pobiner 2015). In
5 some historical hominin-inhabited areas there were a greater number of felids than hyenids.
6 Again, this is significant because hyenas are likely to have left far less flesh on a carcass than
7 a felid such as a sabretooth enabling contemporaneous hominins to benefit (Pobiner 2015).
8 The intelligence, resultant tool-use and cooperative nature of hominins meant they could
9 likely adapt to take on more or less carrion depending on their environment (Moleón et al.
10 2014).

11 In Mesozoic systems some extremely large theropod dinosaurs had a morphology
12 indicative of an ability to process bone e.g. the robust skull and dentition of *T. rex* (Hone
13 and Rauhut 2010). There is direct evidence that *T. rex* did this in the form of distinctive
14 wear marks on its tooth apices (Farlow and Brinkman 1994, Schubert and Ungar 2005) and
15 the presence of bone fragments in its coprolites (Chin et al. 1998). The animal also had an
16 enormous bite force, with one estimate putting it at 57000 Newtons (Bates and Falkingham
17 2012). This is noted as being powerful enough to break open skeletal material (Rayfield et al.
18 2001).

19 Further, much work has focused on the existence of scavenging in dinosaurs by using
20 simple energetics approaches that typically focused on a single species namely *Tyrannosaurus*
21 *rex* (Ruxton and Houston 2003, Carbone et al. 2011) but a recent modelling study
22 investigated the likely prevalence of scavenging across a range of body sizes. In it the authors
23 demonstrated that species of intermediate body masses (approximately 500 kg) would have
24 gained the most benefit from scavenging. This was the result of gut capacity limitations and
25 the effects of competition at the carcass. At the larger extreme this owes to the fact that gut
26 capacity doesn't scale isometrically with body mass so the benefits of greater mass level off;

1 there's only so much food an individual can consume at a single sitting (Calder 1996). For
2 the smaller species, larger competitors would have prevented their access to carrion.

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

17 Scavenging should be particularly attractive to avian predators compared to mammals.
18 Solitary mammalian predators can kill prey up to the same body mass as themselves and
19 sometimes an order of magnitude heavier (e.g. socially hunting lions (Owen-Smith and Mills
20 2008)). In contrast, birds of prey tend to kill prey smaller than themselves (Slagsvold and
21 A Sonerud 2007). This is likely due to their need to kill animals that they can fly away with,
22 as well as the risk of injury being higher (which carries a higher mortality risk) for a bird than
23 a mammal. Scavenging provides a means for birds to exploit species that would otherwise be
24 too big for them to kill.

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).

6 And as we have noted the Azhdarchid pterosaurs were far bigger again, with estimated
7 body masses of over 200 kg (Witton and Habib 2010). Although Witton and Naish (2008)
8 argued that neck inflexibility and straight, rather than hooked jaw morphology points against
9 pterosaurs existing as *obligate* scavengers, Azhdarchid terrestrial proficiency indicates they
10 would have been comfortable foraging on the ground. Indeed, extant Marabou Storks
11 (*Leptoptilos crumenifer*) have a comparable morphology and are noted facultative scavengers
12 (Monadjem et al. 2012) so it is reasonable to believe that certain pterosaurs behaved
13 similarly.

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

23 Shviki (2006) points out that "evolutionary pressures favor detection maximizers relative
24 to toxification minimizers in competitive interactions for carcasses." But the fact remains that
25 overcoming microorganism toxins is still a beneficial adaptation to any scavenger. Avian
26 scavengers have evolved incredibly acidic stomachs that allow them to consume and process

putrefied flesh with no ill effects (Houston and Cooper 1975, Roggenbuck et al. 2014). This adaption is not restricted to vultures though, Grémillet et al. (2012) showed wandering albatrosses (*Diomedea exulans* so-called 'vultures of the seas') had an average pH of 1.5, which enables them to consume fisheries discards. Outside of the birds there is evidence of selection for 'toxification minimizers'. From our earlier arguments we know that ectotherms are limited in their ability to find carrion as quickly as endotherms. This implies later arrivers would benefit especially from well-developed detoxifying apparatus. Shivik (2006) suggests that "specialized oral structures in snakes may have evolved under pressures associated with scavenging." Moreover, some authorities have charted an evolutionary course from basal 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.

1 Osteophagy may have been even more viable during the Mesozoic era because of this skewed
2 body mass distribution of herbivores towards larger sizes (O’Gorman and Hone 2012). When
3 we couple this with the fact that skeletal mass scales greater than linearly with body mass
4 (Prange et al. 1979) there would have been a lot of bone material to consume in the
5 environment provided an animal had the biology to process it (Chure and Fiorillo 1997). As
6 we discussed earlier, this ability is often extremely beneficial to a scavenger.

7 Vultures and eagles tend to soar using thermals and if these air pockets don’t form, say
8 on a cloudy day, the bird is grounded (Mundy et al. 1992). In many habitats (e.g. the arctic)
9 it is simply not possible for sufficiently powerful thermals to form and as a consequence
10 large-bodied vultures cannot exist. The upshot of this is that terrestrial carnivores like bears
11 and wolves take more carrion (DeVault et al. 2003). Certainly, a major difficulty for terrestrial
12 scavengers is competition with vultures. Nocturnal behaviour in the hyaenidae in general has
13 been put forth as an adaptation to reduce competition with these exclusively diurnal birds
14 (Gittleman 2013). If we apply this line of reasoning over evolutionary time-scales, the absence
15 of flying vertebrates in the Palaeozoic may have permitted terrestrial forms to take in a
16 higher proportion of carrion in their diet.

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

22 Staying in the aquatic setting, the phenomenon of occasional bounties of carrion in the
23 form of whale falls has led some researchers to investigate if a scavenger could survive by
24 seeking out these remains exclusively. Ruxton and Bailey (2005) argued that although this is
25 energetically feasible it’s ecologically unlikely. Any animal that could find such whale
26 carcasses is unlikely to have ignored other types of carrion. Although no aquatic species have

1 ever exceeded the size of whales, some enormous animals have evolved in this environment
2 before the evolution of whales, including *Leedsichthys*, a bony fish from the Middle Jurassic
3 (174.1-163.5 Mya), that weighed in excess of 20 tonnes. Thus, the energetic feasibility of a
4 marine scavenger that specialises on large carcasses has a long history. One point of interest
5 is that of the whaling industry, which provided a bonanza of floating carcasses especially
6 during the 20th century (Whitehead and Reeves 2005). This meant Killer Whales (*Orcinus*
7 *orca*) could switch from hunting to scavenging, a switch made that much easier by the noise
8 of the whaling vessels that would effectively ring the "dinner-bells" (Whitehead and Reeves
9 2005). Early whales such as *Basilosaurus* seem to fit into the same niche as Killer Whales
10 and we have some evidence for scavenging in this group as well (Fahlke 2012).

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

1 **Conclusion**

2 As is often the case in science, the present provides the key to the past. The animals of
3 today, while often different (sometimes radically so) to their ancestors, allow us to make
4 informed comparisons to extinct species. We have used this technique to give insight into the
5 drivers of scavenging across terrestrial vertebrates through time. In common with any other
6 forager be they grazer, browser or predator, scavengers past and present have had to balance
7 their energetic costs with the gains of food. Our four main axes: locomotion, detection,
8 processing and environment can be used to create a scale of scavenging whereupon any
9 species can be placed in order to establish the importance of carrion in it diet.

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