Abstract

Despite its prevalence, scavenging is a difficult behaviour to observe in modern day carnivores and impossible to study directly in extinct species. Yet, there are certain intrinsic and environmental features of a species that push it towards a scavenging lifestyle. Chief among these are low-cost locomotion, high detection distances, effective carcass processing and a carrion-producing habitat. We use these four components to highlight the morphologies and environments that would have been conducive to scavenging over geological time by focussing on dominant vertebrate groups of the land, sea and air. The result is a document on the natural history of scavenging, the first to our knowledge. Our idea of a scale of scavenging can be applied to any species at any time to judge the importance of this behaviour in its diet.

1 Introduction

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 (DeVault et al. 2003). Professor Sanborn Tenney writing in 1877 for The American Naturalist 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 (Carbone et al. 2011), 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). This has profound implications for the trophic ecology of these systems and particulary our models of them. 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 (Jones et al. 2015). By recognising the difficulty in directly observing scavenging, other methods have been turned to to discern the most suitable morphologies, physiologies and environments for a scavenging lifestyle to prosper. Here we chart the natural history of scavenging by assessing the potential for the behaviour in dominant vertebrate groups given

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¹ their ecology and functional traits.

The Difficulty of Scavenging

³ The chief hurdle of scavenging is finding a resource that is often difficult to predict in space
⁴ and time. Though chance alone many species will avail of some level of opportunistic
⁵ scavenging opportunities. However, species that rely on scavenging to sustain substantial
⁶ portions of their diets must increase the probability of encountering a sufficient amount of
⁷ carrion in order to meet some energetic demands. Once found, the scavenger must be able to
⁸ out-compete any potential competitors and process a product under the processes of decay
⁹ from toxin producing and disease causing microorganisms (Ruxton et al. 2014). Finally, the
¹⁰ level of scavenging opportunities available will also depend on the density, size, and quality of
¹¹ carcases produced, all of which are dependent on complex ecosystem dynamics. These facets
¹² which are required for scavenging are essentially the key parameters found in the species
¹³ functional response curves of optimal foraging theory, namely encounter rate, handling time
¹⁴ and prey availability (Jeschke et al. 2002). We compare the ability of scavenging across the
¹⁵ vertebrates based on each of these facets and their relationship with scavenging. By framing
¹⁶ scavenging in a framework of optimal foraging and identify the perquisite attributes and
¹⁷ processes required for scavenging we produce a 'scale of scavenging' whereupon we can place
¹⁸ any species, past or present, and assess the importance of scavenging in its diet.

Encounter Rate

²⁰ All foraging processes depend on the encounter rate between consumer and resource. In the
²¹ simplest case, this rate can be thought of in terms of a gas diffusion model where the
²² movement of two agents depends only on their relative speed. As carcasses are stationary,
²³ the relative speed between a scavenger and carrion is dependent on the movement of the

Proportion of scavenging in the diet

Intrinsic influencing factors:
Locomotion cost
e.g. volancy
Detection rate
e.g. vision or olfaction
Food processing
e.g. phenotypic adaptations

Extrinsic influencing factors:
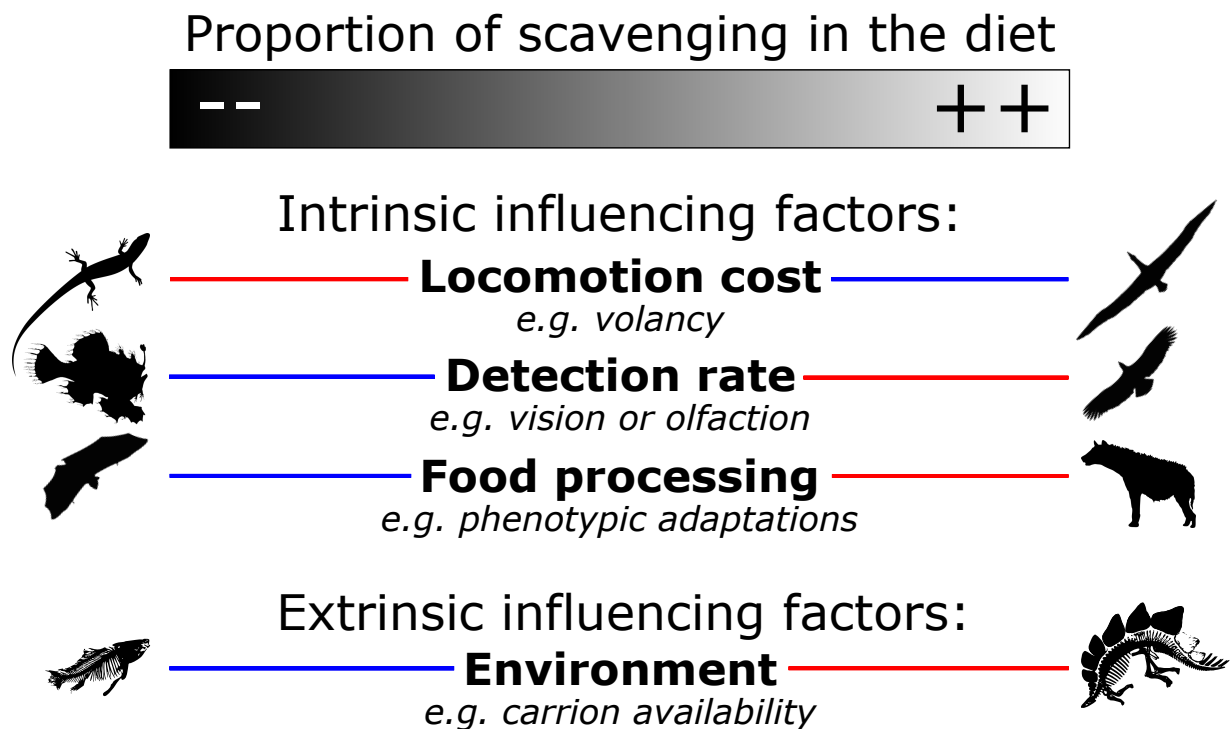### Environment
e.g. carrion availability

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 scavenger. Vertebrates do more than simply bump into resources like gas molecules though,

2 because they can actively detect resources through their sensory abilities. Scavenging will also

3 depend on search rates, which are dependent on both species physiology and the

4 dimensionality of the environment ((Pawar et al. 2012)).

5 **Locomotion**

6 In contrast to the importance of locomotion in predation, locomotion relating to scavenging

7 depends more on the ability to efficiently move over large areas. This ability generally

8 requires an efficient transfer of metabolic energy into movement which relies on both

9 physiology (i.e. metabolism) and the medium of the environment in which the animal is

10 moving (i.e. aerial, aquatic or terrestrial). Perhaps the most efficient form of locomotion in

11 vertebrates is, paradoxically, found in flying species. Despite the energetic costs of flight, the

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only known vertebrate, obligate scavengers are the old and the new world vultures. This is because, although powered flight is energetically expensive, species like vultures can exploit air currents using large wingspans which allows them to soar while only doubling their metabolic rate (Hedenstrom 1993, Spivey et al. 2014). By depending on thermal air flows these species can forage over enormous ranges (Spiegel et al. 2013). This mode of locomotion is also exploited by sea birds, which use strong ocean winds to search large areas of the oceans (Norberg 2012, Thaxter et al. 2012). While many species of seabird are likely primarily predators, it seems that albatrosses, who can range many hundreds of kilometres, take a substantial amount of carrion in their diet (Croxall and Prince 1994). This is typically in the form of squid, which float on the surface, allowing the birds to readily pluck their remains out of the water (Croxall and Prince 1994).

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

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

We know that many extant birds exist as facultative scavengers because storks, raptors and corvids all take substantial quantities of carrion in their diet (Kendall 2013). Similarly we would expect that extinct species would also gain in a similar fashion depending on the efficiency of flight. For example, early birds such as *Archaeopteryx* are predicted to have been poor, relatively inefficient fliers (Nudds and Dyke 2010). Similarly someithing about the effeciny of pterosuars flight. The importance of efficient flying over large areas may explain the lack of scavenging behavior in bats as they are generally noctural, a time when they would receive no aid from convective air currents (Norberg 2012). That said, *Necromatis* ("death-eater"), a large bat from the middle to late Eocene (56 to 33.9 Mya) had a robust cranio-mandibular morphology, and is a likely candidate for scavenging behavior amongst the x amount of known bat species (Weithofer 1887, Hand et al. 2012).

Similar to aerial species, aquatic scavengers have a locomotory benefit because water is a medium that is conducive to low-cost movement (Tucker 1975). In fact, the total cost of movement (again in J kg^{-1} m^{-1}) in fish is lower than either running or flying where it scales according to $2.15 \times$ body mass (kg) $^{-0.25}$ (Williams 1999) with only *soaring* flight likely to surpass it. This has led some researchers to argue for the feasibility of an obligate scavenging fish (Ruxton and Houston 2004a, Ruxton and Bailey 2005). Sharks perhaps best resemble the large soaring fliers as they depend on large pectoral fins in order to maintain lift as they swim. Many shark species show very large ranges (e.g. great white sharks (*Carcharodon carcharias*)) and have the lowest cost of swimming (I know the Greenland shark is the slowest swimmer). Faculative scavenging is seen in many marine groups including species of extant sharks such as White sharks, that are known to feed on whale carcasses (Fallows et al. 2013), Greenland sharks feeding on seals (Watanabe et al. 2012), and sixgill sharks (Anderson and Bell 2016). There is evidence too of scavening in extinct species, where shark teeth have been found in the remains of dinosaurs, mososaurs and 4-million-year-old mysticete whales (Schwimmer et al. 1997, Ehret et al. 2009).

We might expect then that by combining an aquatic environment and an endothermic metabolism marine mammals would prosper as scavengers. Fossil pinnipeds and cetaceans from 60 Mya have transitional features indicative of their trajectory to fully aquatic species (Williams 1999). But despite their movement away from land their energetic savings were negligible because the *total* cost incurred by a swimming marine mammal is high (Williams 1999). Indeed, the total energetic cost is similar to an equivalent terrestrial or aerial mammal (Williams 1999). This underscores the trade offs between the benefits of endothermy in terms of activity periods and the costs of maintaining such an expensive system.

Terrestrial environments are the most energetically costly in which to move, because an animal must trade off the cost of supporting its body off the ground while propelling itself forward. The idea that the evolutionary transition in posture from the sprawling gait of reptiles to the erect posture of mammals conferred a huge advantage to the latter is often repeated e.g. benefits in terms of speed, efficiency, muscle effort and maneuverability (Sullivan 2015). Yet, as Sullivan (2015) states, most of the hypotheses in favour of this idea remain to be tested in the context of archosaur evolution. Although, metabolic rate unquestionably impacts terrestrial species whereby ectotherms such as many modern reptiles, cannot move for sustained periods (Bennett and Ruben 1979). This is exacerbated by their sprawling gait which results in the phenomenon known as 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 would also be true of extinct species. It is during the Permian (298.9 - 252.17 Mya) 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). Snakes are a bit different are more effecent at moving I think - lots of scavanging. Both these groups are more likely to depend on low energetic costs in order to componsate for low ecnounter rates duee to thier inabilty to move. It is with the evolution of endothermy in the therapsid-mammal lineage (Clarke and Pörtner 2010) that terrestrial

vertebrates would have gained the ability to range more widely, a vital component in seeking out carrion.

Modern endothermic mammals can sustain longer periods of energetically expensive activity (Bennett and Ruben 1979) resulting in larger foraging ranges. 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 $1.15 \times$ body mass (kg) $^{0.12}$ and $0.23 \times$ body mass (kg) $^{0.12}$ respectively (Ruxton and Houston 2004b). If we insert these into a foraging radius model $\frac{duration \times speed}{2}/1000$ 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 between the ambush strategies of cats and the pursuit/ pounce strategies of dogs, the latter being more suited to scavenging (Janis and Figueirido 2014). We can (and have) use(d) these insights to compare extant terrestrial species to their prehistoric forebears given the

dominance of mammalian carnviores since the Eocene (56-33.9 Million years ago; Mya) where
the order split into the Caniforma and Feliforma (Van Valkenburgh 1987). To take one
example, Anyonge (1996) found that *Nimravides*, a genus of sabretooth cat from the
Miocence (10.3 to 5.3 Mya) were likely to have been ambush predators which would argue
against them taking a lot of carrion.

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

Unsurprisingly, given their enduring appeal, the prevalence of scavenging has been
explored in the carnivorous, theropod dinosaurs. They were the dominant terrestrial
carnivores for most of the Mesozoic Era (252.17 - 66 Mya) and 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.

Detection

It would be pointless to have incredible ranging abilites 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). If we compare this to the energetics approach by Ruxton and Houston

(2004b), they calculated a terrestrial scavenger needs to be able to detect carrion at 500 m

in order to survive, which is clearly within the ability of hyenas. Moreover, the senses of many

extant (and in all probabilty 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). We can

contrast this ability with bats, whose visual acuity is famously poor. It also appears that

echolocation would not lend itself to discovering immobile carrion. Their small size and poor

terrestrial ability would also count against them at a carcass (Riskin et al. 2006).

Having a panoramic view means being able to gather a wealth of information from other

foragers, be they conspecifics or otherwise (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).

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

In contrast to the air, aquatic species have to contend with the low-light environment of water where visual detection distances are far lower (< 100 m) than they would be in the air. As such, animals here detect resources through chemo- and mechanoreception more so than through vision (Ruxton and Houston 2004a). This is particularly relevant to extant sharks and aquatic snakes who are deemed as having the most suitable physiology for scavenging. A hypothesis 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 preponderence 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.

Handling Time

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 and others reveals another useful scavenger trait. Osteophagy is known across a range of terrestrial carnivores and given some fat-rich mammalian bones have

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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). Indeed, their extinction has been blamed on the decline of sabretooth

cats (Machairodontinae), the unique skull morphology of the latter meant they would leave a

large amount of food on a carcass for would-be scavengers (Palmqvist et al. 2011). Earlier in

the evolution of mammals, 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).

Certainly, scavenging should be particularly attractive to avian predators compared to

mammals. The latter can kill prey up to the same body mass as themselves and sometimes

an order of magnitude heavier (e.g. socially hunting lions; Owen-Smith and Mills 2008). In

contrast, birds of prey tend to kill prey smaller than themselves (Slagsvold and A Sonerud

2007) because of the greater cost of injury and need to carry off their food. Scavenging

provides a means for birds to exploit species that would otherwise be too big for them to kill.

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 (Domínguez-Rodrigo 2002). 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. Again, this is significant because hyenas are likely to have left

far less flesh on a carcass than a felid such as a sabretooth enabling contemperaneous

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).

In Mesozoic systems some extremely large theropod dinosaurs had a morphology indicative of 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).

Further, 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 prevelance of scavenging across a range of body sizes. In it the authors demonstrated that species of intermediate body masses (approximatively 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 addition to reducing locomotory costs we would expect adaptations that reduce energetic costs of maintenance to be selected for in scavengers because it would maximise the benefit derived from such a sporadic food source. Extant reptiles possess an advantage here, in that over the course of a year their food requirements can be 30 times lower than an endotherm of equal size (Nagy 2005). 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 crocodlies and their allies (Forrest 2003). A sit and wait strategy is viable for an ectotherm. This low existence cost is also realised in many sharks who have coupled low locomotory costs with an ectothermic metabolism. The upshot is that 30 kg of blubber can sustain a White shark for over six weeks (Carey et al. 1982).

Large body size confers substantial dominance and starvation-resistance benefits (Ruxton and Houston 2004b). Thus, we would expect scavengers to have this trait selected for even in the case of weight-constrained fliers. Wandering Albatrosses (*Diomedea exulans*), Cinereous Vultures (*Aegypius monachus*) and condors (*Vultur gryphus*, *Gymnogyps californianus*) all have body masses that can exceed 10 kg and represent some of the heaviest bird species capable of flight (Weimerskirch 1992, Ferguson-Lees and Christie 2001, Donázar et al. 2002).

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

The competitive ability of even the largest bird is radically diminished in their interactions with mammalian competitors however, and as such they tend to consume carrion rapidly. Houston (1974) observed a group of *Gyps* vultures consuming all of the soft tissue from a 50

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kg Grant's gazelle (*Nanger granti*) in eight minutes. Their serrated tongues and hooked bills

enabling them to achieve this feat (Houston and Cooper 1975). Outside of raptors such as

vultures, the specialised beaks of many modern bird lineages hinders their ability to eat meat

which is in contrast to the first lineages that did not have this feature (Martyniuk 2012) . As

Martyniuk (2012) notes these early birds would thus have been predominantly carnivorous,

which implies that scavenging would have been a live opportunity cf. their descendants.

Although the observation of Shivik (2006) that "evolutionary pressures favor detection

maximizers relative to toxification minimizers in competitive interactions for carcasses."

appears sound, the fact remains that overcoming microorganism toxins is still a beneficial

adaptation to any scavenger. Avian scavengers have evolved incredibly acidic stomachs that

allow them to consume and process putrefied flesh with no ill effects (Houston and Cooper

1975, Roggenbuck et al. 2014). This adapation is not restricted to vultures though, Grémillet

et al. (2012) showed wandering albatrosses (*Diomedea exulans*; so-called 'vultures of the

seas') had an average pH of 1.5, which enables them to consume fisheries discards and squid

carcasses. There is also evidence of selection for 'toxification minimizers' beyond birds among

the ectotherms. From our earlier arguments we know that ecthotherms 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 (Aguirre et al. 2003).

1 Prey Availability

Both the biotic and abiotic environment a would-be scavenger finds itself in can influence to degree to which it can depend on carrion. Ruxton and Houston (2004b) suggest a system similar to the Serengeti in productivity could have supported a mammalian or reptilian 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 herbviores 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 and wolves take more carrion (DeVault et al. 2003). Certainly, a major difficulty for terrestrial scavengers is competition with vultures. Noctural behaviour in the hyaenidae in general has been put forth as an adaptation to reduce competition with these exclusively diurnal birds (Gittleman 2013). If we apply this line of reasoning over evolutionary time-scales, the absence

of flying vertebrates in the Palaeozoic may have permitted terrestrial forms to take in a higher proportion of carrion in their diet.

Staying in the aquatic setting, the phenomenon of occasional bounties of carrion in the form of whale falls has led some researchers to investigate if a scavenger could survive by seeking out these remains exclusively. Ruxton and Bailey (2005) argued that although this is energetically feasible it's ecologically unlikely. Any animal that could find such whale carcasses is unlikely to have ignored other types of carrion. Although no aquatic species have ever exceeded the size of whales, some enormous animals have evolved in this environment before the evolution of whales, including *Leedsichthys*, a bony fish from the Middle Jurassic (174.1-163.5 Mya), that weighed in excess of 20 tonnes. Thus, the energetic feasiblity of a marine scavenger that specialises on large carcasses has a long history. One point of interest is that of the whaling industry, which provided a bonanza of floating carcasses especially during the 20th century (Whitehead and Reeves 2005). This meant Killer Whales (*Orcinus orca*) could switch from hunting to scavenging, a switch made that much easier by the noise of the whaling vessels that would effectively ring the "dinner-bells" (Whitehead and Reeves 2005). Early whales such as *Basilosaurus* seem to fit into the same niche as Killer Whales 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 over time. 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, can be used 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. The main factors we considered namely, encounter rate, handling time and prey availability can be used to create a scale of scavenging whereupon any species can be placed in order to establish the importance of carrion in it diet. We hope this approach will be useful in the effort to explore this most understudied of feeding ecologies.

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