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

6 Adam Kane, Kevin Healy, Thomas Guillerme, Graeme Ruxton, & Andrew Jackson.

7 1. A. Kane (*adam.kane@ucc.ie*), University College Cork, Cooperage Building, School
8 of Biological Earth and Environmental Sciences, Cork, Ireland.

9 2. K. Healy and A. Jackson, Trinity College Dublin, Department of Zoology, School of
10 Natural Sciences, Dublin Ireland.

11 3. T. Guillerme, Imperial College London, Silwood Park Campus, Department of Life
12 Sciences, Buckhurst Road, Ascot SL5 7PY, United Kingdom.

13 4. G. Ruxton, School of Biology, Sir Harold Mitchell Building, Greenside Place, St
14 Andrews, KY16 9TH, United Kingdom.

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. These can be thought of as some of the principal parameters in optimal foraging theory namely, encounter rate, handling time and prey availability. We use these components to highlight the morphologies and environments that would have been conducive to scavenging over geological time by focussing on the dominant vertebrate groups of the land, sea and air. The result is a document on the natural history of scavenging, the first to our knowledge. Our idea of a scale of scavenging can be applied to any species at any time to judge the importance of this behaviour in its diet.

1 Introduction

2 Historically, scavengers have not been viewed as the most charismatic of animals. This may
3 go some way to explaining the gap in our knowledge of the prevalence of this behaviour
4 (DeVault et al. 2003). Professor Sanborn Tenney writing in 1877 for *The American Naturalist*
5 had this to say about one well known group, "prominent among the mammalian scavengers
6 are the hyenas, the ugliest in their general appearance of all the flesh eaters." He contrasts
7 these with "nobler kinds" of carnivores such as lions and tigers (Tenney 1877). Even aside
8 from our own subjective biases, scavenging is a difficult behaviour to detect after the fact.
9 Without catching a carnivore in the act of killing we are left to infer how the prey was killed.
10 Some simple heuristics can inform us, for instance, in cases where the prey item was simply
11 too large to have been killed by the ostensible predator (Pobiner 2008). But clearly, a
12 scavenger doesn't only feed on animals too big for it to have hunted. The obvious lack of
13 direct behavioural data compounds the difficulty of discerning scavenging among extinct
14 forms. Indeed, a single species of dinosaur notwithstanding (Carbone et al. 2011), a synthesis
15 describing the natural history of scavengers is absent from the literature. Fortunately,
16 research on scavenging is on the rise (Koenig 2006). As a result, we are now beginning to
17 realise the extent of this behaviour such that, "in some ecosystems, vertebrates have been
18 documented to assimilate as much as 90% of the available carrion" (Beasley et al. 2015).
19 This has profound implications for the trophic ecology of these systems and particularly our
20 models of them. Even Tenney's noble big cats are now known to take in a significant portion
21 of carrion in their diet where some lion populations get over 50% of their meat from
22 carcasses (Jones et al. 2015). By recognising the difficulty in directly observing scavenging,
23 other methods have been turned to to discern the most suitable morphologies, physiologies
24 and environments for a scavenging lifestyle to prosper. Here we chart the natural history of
25 scavenging by assessing the potential for the behaviour in dominant vertebrate groups given

1 their ecology and functional traits.

2 **The Difficulty of Scavenging**

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

17 **Encounter Rate**

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

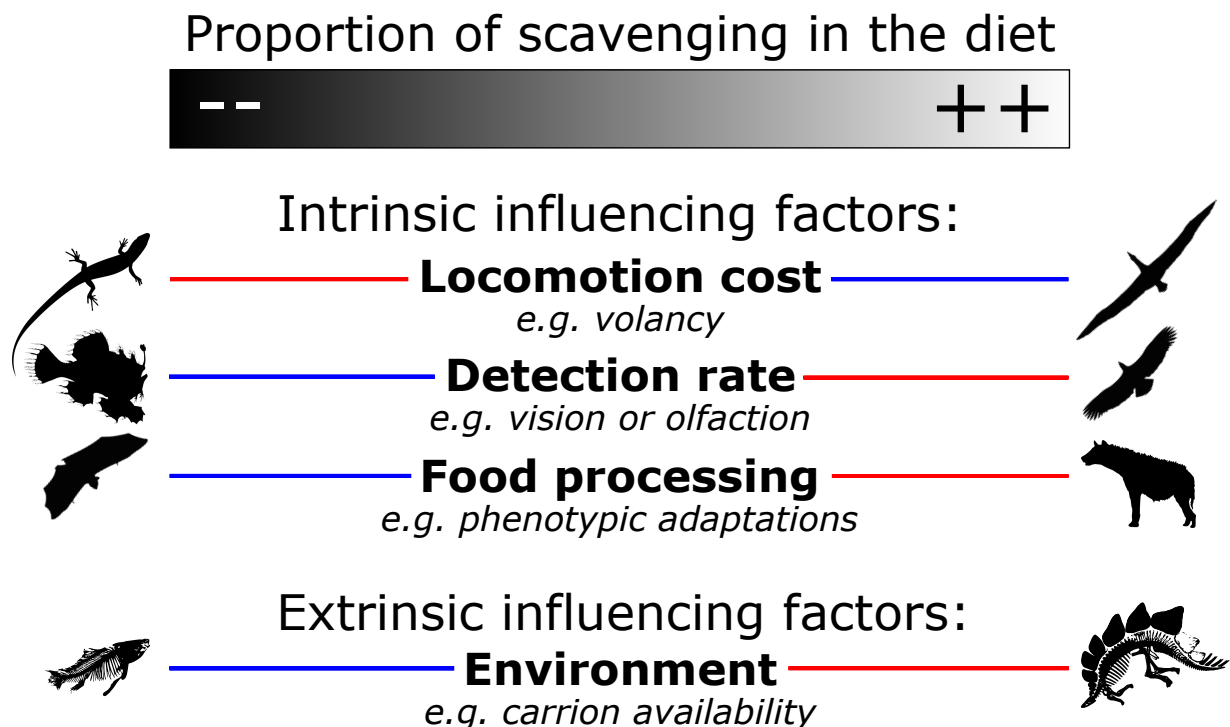


Figure 1: Factors influencing the proportion of scavenging in a vertebrates' diet. Blue lines indicates a reduction in the factor and red lines indicates an increase.

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

3 **Locomotion**

4 Scavenging depends more on the ability to efficiently move over large areas than does
 5 predation because of the inherent unpredictability of carrion. This generally requires an
 6 efficient transfer of metabolic energy into movement which relies on both physiology (i.e.
 7 metabolism) and the medium of the environment in which the animal is moving (i.e. aerial,
 8 aquatic or terrestrial). Perhaps the most efficient form of locomotion in vertebrates is,
 9 paradoxically, found in flying species. Despite the energetic costs of flight, the only known
 10 vertebrate obligate scavengers are the old and the new world vultures. And, although
 11 powered flight is energetically expensive, species like vultures can exploit air currents using

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

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

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

25 We know that many extant birds exist as facultative scavengers because storks, raptors
26 and corvids all take substantial quantities of carrion in their diet (Kendall 2013). Similarly we

1 would expect that extinct species would also scavenge in a similar fashion depending on the
2 efficiency of their flight. For example, early birds such as *Archaeopteryx* are predicted to have
3 been poor, relatively inefficient fliers (Nudds and Dyke 2010) and so ill-suited to finding
4 carrion. The importance of efficient flying over large areas may explain the lack of scavenging
5 behaviour in bats as they are generally nocturnal, a time when they would receive no aid from
6 convective air currents (Norberg 2012). That said, *Necromantis* (“death-eater”), a large bat
7 from the middle to late Eocene (56 to 33.9 Mya) had a robust cranio-mandibular
8 morphology, and is a likely candidate for scavenging behaviour (Weithofer 1887, Hand et al.
9 2012).

10 Similar to aerial species, aquatic scavengers have a locomotory benefit because water is a
11 medium that is conducive to low-cost movement (Tucker 1975). In fact, the total cost of
12 movement (again in $\text{J kg}^{-1} \text{m}^{-1}$) in (salmonid) fish is lower than either running or flying where
13 it scales according to $2.15 \times \text{body mass (kg)}^{-0.25}$ (Williams 1999) with only *soaring* flight
14 likely to surpass it. This has led some researchers to argue for the likelihood of an obligate
15 scavenging fish (Ruxton and Houston 2004a, Ruxton and Bailey 2005). Interestingly, style of
16 swimming in fish does not significantly affect the cost of movement (Williams 1999).
17 Though sharks perhaps best resemble the large soaring fliers as they depend on large pectoral
18 fins in order to maintain lift as they swim. Many shark species show large ranges, e.g. great
19 white sharks (*Carcharodon carcharias*) (Bruce et al. 2006), and it seems reasonable that they
20 would use oceanographic currents to further reduce movement costs (Ruxton and Houston
21 2004a). Facultative scavenging is seen in many marine groups, including species of extant
22 sharks like white sharks (known to feed on whale carcasses; Fallows et al. 2013), Greenland
23 sharks (feeding on seals; Watanabe et al. 2012), and sixgill sharks (Anderson and Bell 2016).
24 The former which grow up to 6 metres long, can be sustained by 30 kg of whale blubber for
25 over six weeks (Carey et al. 1982). There is evidence too of scavenging in extinct species,
26 where shark teeth have been found in the remains of dinosaurs, mosasaurs and Pliocene (5.3

1 to 3.6 Mya) mysticete whales (Schwimmer et al. 1997, Ehret et al. 2009).

2 We might expect then that by combining an aquatic environment and an endothermic
3 metabolism marine mammals would especially prosper as scavengers. Fossil pinnipeds and
4 cetaceans from 60 Mya have transitional features indicative of their trajectory to fully aquatic
5 species (Williams 1999). But despite their movement away from land their energetic savings
6 were negligible because the *total* cost incurred by a swimming marine mammal is high
7 (Williams 1999). Indeed, the total energetic cost is similar to an equivalent terrestrial or
8 aerial mammal (Williams 1999). This underscores the trade offs between the benefits of
9 endothermy in terms of activity periods and the costs of maintaining such an expensive
10 system. That said, aquatic endotherms have and do scavenge. For instance, early whales
11 such as *Basilosaurus* (38 to 36.5 Mya) seem to fit into the same niche as killer whales
12 (*Orcinus orca*) and we have some evidence for scavenging in both (Fahlke 2012, Whitehead
13 and Reeves 2005).

14 Terrestrial environments are the most energetically costly in which to move, which may be
15 due to the low muscular efficiency of running (Tucker 1975) as well as the relative inefficiency
16 of gas exchange in mammals cf. birds and fish (Williams 1999). The idea that the
17 evolutionary transition in posture from the sprawling gait of reptiles to the erect posture of
18 mammals conferred a huge advantage to the latter is often mentioned. The purported
19 advantages include benefits in terms of speed, efficiency, muscle effort and manoeuvrability
20 (Sullivan 2015). Despite being intuitive, as Sullivan (2015) states, most of the hypotheses in
21 favour of this idea remain to be tested in the context of archosaur evolution. Metabolic rate
22 however, unquestionably impacts terrestrial species whereby ectotherms such as many modern
23 reptiles, cannot move for sustained periods (Bennett and Ruben 1979). This is exacerbated
24 by their sprawling gait which results in the phenomenon known as Carrier's constraint such
25 that the animal can't move and breathe at the same time because the lateral movements
26 impedes its lungs (Carrier 1987). This would also have been true of extinct species with the

1 same physiology. It is with the evolution of endothermy in the therapsid-mammal lineage
2 (Clarke and Pörtner 2010) that terrestrial vertebrates would have gained the ability to range
3 more widely, a vital component in seeking out carrion. Although the earliest evidence of
4 vertebrate scavenging comes from the Permian (298.9 - 252.17 Mya) where a temnospondyl
5 amphibian fed on the carcass of *Varanops*, a predatory synapsid of the time (Reisz and Tsuji
6 2006).

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

14 Today, terrestrial scavenging in the mammals is probably best known in an African
15 context where hyenas, jackals and lions all take sizeable proportions of carrion in their diet.
16 In the spotted hyena (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*) and brown hyena
17 (*Hyaena brunnea*) it can be over 90% (Jones et al. 2015). And although no contemporary
18 terrestrial vertebrate exists as an obligate scavenger, most, if not all, are facultative to some
19 extent (Beasley et al. 2015). The particular reliance of hyenas on carrion means we can use
20 them as examples of efficient terrestrial scavengers to compare with other forms. In terms of
21 locomotion, they employ a characteristic "rocking horse gait" which allows them to cover
22 great distances efficiently, loping at 10 km/hr (Mills 1989, Jones et al. 2015). Such
23 long-distance travel is apparent in African wild dogs (*Lycaon pictus*) and many other canids
24 (Pennycuick 1995, Janis and Figueirido 2014). In contrast, big cats like leopards (*Panthera*
25 *pardus*) rely on ambush (Pennycuick 1995). This allows us to make a broad distinction
26 between the ambush strategies of cats and the pursuit/ pounce strategies of dogs, the latter

1 being more suited to scavenging (Janis and Figueirido 2014). These insights allow us to
2 compare extant terrestrial species to their prehistoric forebears given the dominance of
3 mammalian carnivores since the Eocene (56-33.9 Million years ago; Mya) where the order
4 split into the Caniforma and Feliforma (Van Valkenburgh 1987). To take one example,
5 Anyonge (1996) found that *Nimravides*, a genus of sabretooth cat from the Miocene (10.3
6 to 5.3 Mya), were likely to have been ambush predators which would argue against them
7 taking a lot of carrion.

8 Although the evolution of bipedal movement was significant in that it freed up the
9 forelimbs for other purposes e.g. climbing, tool-use, wing development etc. it does not differ
10 radically in cost from quadrupedal locomotion (Williams 1999, and references therein). For
11 instance, Alexander (2004) shows that, in the case of humans, we are more economical than
12 predicted while walking and less so while running according to predicted costs of terrestrial
13 movement.

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

Detection

It would be pointless to have incredible ranging abilities and not have the sensory architecture to benefit from it. As predicted by the necessity of an increased encounter rate, scavengers have well-developed senses. 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). We can compare this to the energetics approach of Ruxton and Houston (2004b), who calculated a terrestrial scavenger needs to be able to detect carrion at 500 meters in order to survive, which is clearly within the ability of hyenas. Moreover, 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. Certainly, 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 vision (Reymond 1985). It follows 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 with many bats whose reliance on echolocation would not lend itself to discovering immobile carrion.

Having a panoramic view also means being able to gather a wealth of information from other foragers, be they conspecifics or otherwise (Jackson et al. 2008). Again, returning to

1 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). This efficiency has been exploited by mammals such as hyenas
5 who are known to follow groups of vultures (Jones et al. 2015).

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

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

Handling Time

Since the food a scavenger depends on is not dispatched directly, often the most easily accessible and choicest components of the carcass will be missing or, if present, will be subject to decay as well as competition. So being able to overcome competitors, maximise the nutrient gain from the remnants, and survive long enough between meals are all essential parts of carcass handling time.

In the ability to eat bone scavengers have arrived at a way to feed on a resource that is typically too hard for many predators to process. Osteophagy is known across a range of terrestrial carnivores and given that 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). 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 (Borophaginae; 33.9 - 23.03 Mya) have also been compared to hyenas in terms of their feeding ecology (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 (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*

1 *erectus* (Pobiner 2015). In some historical hominin-inhabited areas there were a greater
2 number of felids than hyenids. Again, this is significant because hyenas are likely to have left
3 far less flesh on a carcass than a felid such as a sabretooth, enabling contemporaneous
4 hominins to benefit (Pobiner 2015). The use of tools and the cooperative nature of hominins
5 meant they could likely get a substantial part of their energetic requirements through
6 scavenging depending on their environment (Moleón et al. 2014).

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

15 We know that large body size confers substantial dominance and starvation-resistance
16 benefits (Ruxton and Houston 2004b). As such, theropod dinosaurs, who could get up to 15
17 tonnes, would seem likely candidates for scavenging. Much work has focused on the existence
18 of scavenging in dinosaurs by using simple energetics approaches that typically focused on a
19 single species namely *T. rex* (Ruxton and Houston 2003, Carbone et al. 2011) but a recent
20 modelling study investigated its prevalence across a range of body sizes.

21 In their work, the authors demonstrated that species of *intermediate* body masses
22 (approximatively 500 kg) would have gained the most benefit from scavenging. This was the
23 result of gut capacity limitations and the effects of competition at the carcass. At the larger
24 extreme this owes to the fact that gut capacity doesn't scale isometrically with body mass so
25 the benefits of greater mass level off; there's only so much food an individual can consume at
26 a single sitting (Calder 1996). For the smaller species, larger competitors would have

1 prevented their access to carrion.

2 The support of water allows for many aquatic species to reach large sizes thus granting its
3 benefits. Collins et al. (2005) found "contrasting relationships between size (body mass) and
4 depth in the scavenging and predatory demersal ichthyofauna". Predatory species saw a
5 reduction in body mass with depth whereas the reverse trend was true for scavengers. This,
6 the authors pointed out, is because randomly distributed carrion is better exploited by fish
7 with larger body sizes owing to starvation resistance.

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

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

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

11 Because of the random nature of carrion we would expect adaptations that reduce
12 energetic costs of maintenance to be selected for in scavengers as it would maximise the
13 benefit derived from such a sporadic food source. Extant reptiles possess an advantage here,
14 in that over the course of a year their food requirements can be 30 times lower than an
15 endotherm of equal size (Nagy 2005). DeVault and Krochmal (2002) suggest this is an
16 avenue for scavenging in snakes because they "exhibit exceedingly low maintenance
17 metabolisms, and most can survive on a few scant feedings per year. It is, therefore, possible
18 for snakes to rely largely on infrequent, less energy-rich meals." In the same review the
19 authors found occurrences of scavenging spread across five families of snakes and stated that
20 this behaviour is "far more common than currently acknowledged." (DeVault and Krochmal
21 2002). The same reasoning can be applied to crocodiles and their allies (Forrest 2003)
22 because a sit and wait strategy is viable for an ectotherm.

23 Although the findings of Shivik (2006) that "evolutionary pressures favor detection
24 maximizers relative to toxification minimizers in competitive interactions for carcasses."
25 appears sound, the fact remains that overcoming microorganism toxins is still a beneficial
26 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 adaptation 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 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 researchers have suggested an evolutionary course from basal fossorial snakes to modern terrestrial species by way of an obligate scavenger intermediate (Bauchot 2006).

Conversely, entire clades appear to lack many, if not all, of these phenotypic adaptations. For example, the extant bats appear to lack most of the features we have identified as important in reducing handling time. The larger forms (which are better suited for scavenging, following our previous arguments) are typically frugivores and therefore lack the adaptations for digesting meat. While the smaller carnivorous bats are mainly found in the microbats which are insectivorous (Aguirre et al. 2003). Additionally, their poor terrestrial ability and cost of movement on the ground would also count against them when feeding at a carcass (Riskin et al. 2006, Voigt et al. 2012).

Prey Availability

The position of a species on the scavenging scale can also be influenced by the availability of carrion in the environment, which is dependent on biotic and abiotic factors. Aspects including, primary productivity, relief, temperature and competition will all greatly affect

1 scavenging tendency. Ruxton and Houston (2004b) suggest a system with a productivity
2 similar to the Serengeti could have supported a mammalian or reptilian terrestrial scavenger.
3 Indeed, in systems that were dominated by large ectothermic or mesothermic vertebrates, the
4 same primary productivity would have supported a greater biomass (McNab 2009). The
5 upshot of this is that there was a higher biomass of herbivores dying and offering scavenging
6 opportunities. Predators were large-bodied too compared to extant mammalian predators
7 (McNab 2009), and so, especially if they were ectothermic, could last longer between meals,
8 rendering scavenging a more attractive behaviour relative to predation. Osteophagy may have
9 been even more viable during the Mesozoic era as well because of this skewed body mass
10 distribution of herbivores towards larger sizes (O’Gorman and Hone 2012). When we couple
11 this with the fact that skeletal mass scales greater than linearly with body mass (Prange
12 et al. 1979) there would have been a lot of bone material to consume in the environment
13 provided an animal had the biology to process it (Chure and Fiorillo 1997).

14 Frequently, the interplay between abiotic and biotic factors can impact the ability of an
15 animal to scavenge. We know vultures and eagles tend to soar using thermals and if these air
16 pockets don’t form, say on a cloudy day, the bird is grounded (Mundy et al. 1992). In many
17 habitats (e.g. the Arctic) it is simply not possible for sufficiently powerful thermals to form
18 and as a consequence large-bodied vultures cannot exist. One result of this is that terrestrial
19 carnivores like bears and wolves take more carrion (DeVault et al. 2003). Certainly, a major
20 difficulty for terrestrial scavengers is competition with vultures. Nocturnal behaviour in the
21 hyaenidae in general has been put forth as an adaptation to reduce competition with these
22 exclusively diurnal birds (Gittleman 2013). If we apply this line of reasoning over evolutionary
23 time-scales, the absence of flying vertebrates in the Palaeozoic may have permitted terrestrial
24 forms to take in a higher proportion of carrion in their diet.

25 In fact, scavenging behaviour may have evolved on land as soon as the first terrestrial
26 tetrapods emerged. Some of the earlier tetrapods tracks dating back to the early Middle

1 Devonian (393.3 - 387.7 Mya) were found in intertidal environments (Niedzwiedzki et al.
2 2010). These environments are isolated from marine systems twice a day leaving potential
3 carrion unexploited by marine vertebrates. Niedzwiedzki et al. (2010) suggest that these
4 environments "would thus have allowed marine ancestors of tetrapods gradually to acquire
5 terrestrial competence while accessing a new and essentially untouched resource."

6 Staying in the aquatic setting, the phenomenon of occasional bounties of carrion in the
7 form of whale falls has led some researchers to investigate if a scavenger could survive by
8 seeking out these remains exclusively. Ruxton and Bailey (2005) argued that although this is
9 energetically feasible it's ecologically unlikely. Any animal that could find such whale
10 carcasses is unlikely to have ignored other types of carrion. Although no aquatic species have
11 ever exceeded the size of whales, some enormous animals have evolved in this environment
12 before the evolution of cetaceans, including *Leedsichthys*, a bony fish from the Middle
13 Jurassic (174.1-163.5 Mya) and the aquatic Mesozoic reptiles, the plesiosaurs, pliosaurs and
14 ichthyosaurs, that could all exceed 15 metres in length (Ruxton 2011). So, despite being
15 unlikely, the energetic feasibility of a marine scavenger that specialises on large carcasses has
16 a long history. One point of interest is that of the whaling industry, which provided a
17 bonanza of floating carcasses especially during the 20th century (Whitehead and Reeves
18 2005). This meant killer whales could switch from hunting to scavenging, a switch made that
19 much easier by the noise of the whaling vessels that would effectively ring the "dinner-bells"
20 (Whitehead and Reeves 2005).

21 Perhaps the greatest environmental driver of scavenging tendency is that of temperature.
22 The geological record shows the Earth has undergone radical fluctuations in temperature over
23 time. This will have had a significant bearing on the availability and persistence of carrion.
24 To illustrate the point, a 10°C increase in ambient temperature can double carcass
25 decomposition rates (Parmenter and MacMahon 2009) and geological evidence indicates that
26 the Mesozoic Earth was on average at least 6 °C warmer than now (Sellwood and Valdes

1 2006). In terms of specific habitats, it has been shown that decomposition is greater in warm
2 and moist areas versus more xeric ones (Beasley et al. 2015). Moreover, oceanic productivity
3 and habitat structure are all impacted by climactic conditions. The impacts these can have
4 on scavengers have been empirically supported e.g. Beasley et al. (2015) who point to a
5 series of studies showing how microbes and invertebrates benefit at higher temperatures to
6 the detriment of vertebrate scavengers such that "above 20°C vertebrates were able to detect
7 and consume only 19% of small-mammal carcasses, whereas at temperatures below 18°C,
8 vertebrates consumed 49% of carcasses". This is a sobering thought given the impact we
9 humans are having on the Earth's climate.

10 **Conclusion**

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

1 **Appendix**

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

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