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

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Abstract

Despite its prevalence, scavenging is a difficult behaviour to observe in modern day carnivores 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 Challenges 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 (i.e. predator and prey) depends only on their relative speed.
21 Vertebrates do more than simply bump into resources like gas molecules though, because
22 predators can actively detect prey through their sensory abilities. As carcasses are stationary,
23 the relative speed between a scavenger and carrion is only dependent on the movement of the

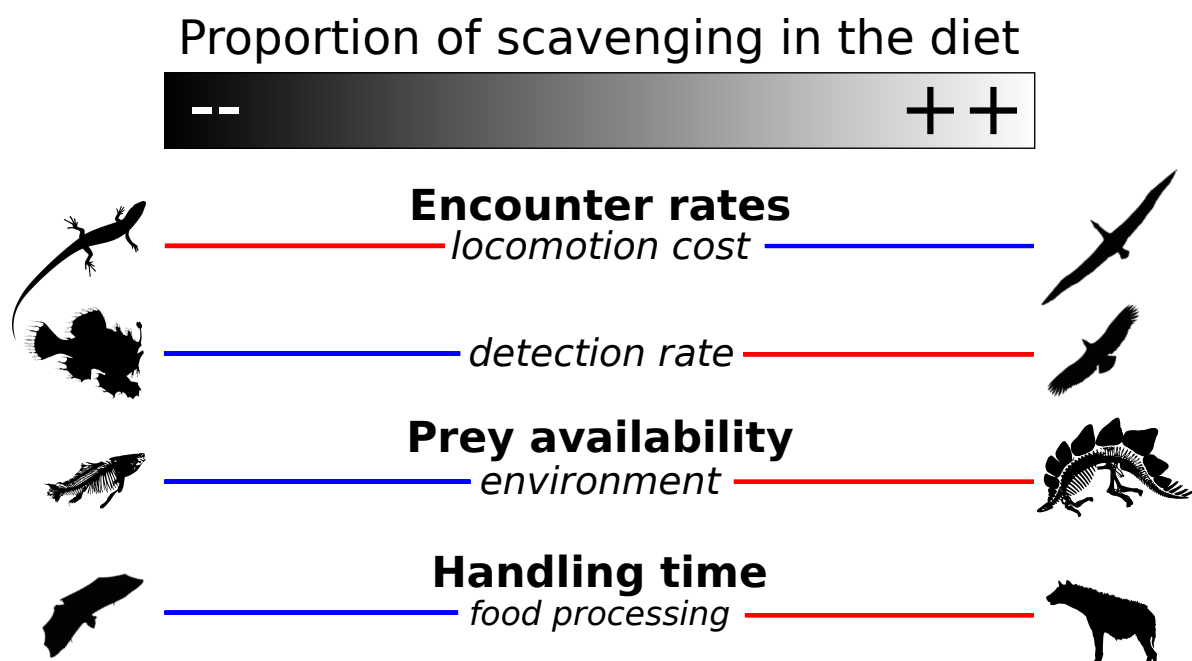


Figure 1: Factors influencing the proportion of scavenging in a vertebrates' diet. Blue lines indicates a reduction in the factor and red lines indicates an increase.

scavenger. As such, scavenging potential is strongly affected by search rates, which are determined by both species' physiology and the dimensionality of the environment (Pawar et al. 2012).

Locomotion

Because of the inherent unpredictability of carrion, scavenging depends more on the ability to efficiently move over large areas than predation. This generally requires an efficient transfer of metabolic energy into movement which relies on both physiology (i.e. metabolism) and the medium of the environment in which the animal is moving (i.e. aerial, aquatic or terrestrial). Perhaps the most efficient form of locomotion in vertebrates is, paradoxically, found in flying species. Despite the energetic costs of flight, the only known vertebrate obligate scavengers are the old and the new world vultures. And, although powered flight is energetically expensive, species like vultures can exploit air currents using their large wingspans which allows them to soar at a cost of only twice their metabolic rate (Hedenstrom 1993, Spivey et al. 2014). By depending on thermal air flows these species can forage over vast ranges (Spiegel et al. 2013). An analogous mode of locomotion is also exploited by seabirds, who 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 carcasses, which float on the surface, allowing the birds to readily pluck their remains out of the water (Croxall and Prince 1994).

The groups from which modern vultures and seabirds arose, appear during the Palaeocene (66 - 56 Million years ago (Mya); Jetz et al. 2012, Jarvis et al. 2014) and Cretaceous (Chiappe and Dyke 2006) respectively. 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

1 the Late Triassic (235-201.3 Mya) coincident with the pterosaurs. Indeed, scavenging among
2 pterosaurs has been hypothesised many times before (Witton and Naish 2008). Certain
3 groups of these animals could reach enormous sizes (e.g. Azhdarchids with wingspans of 11
4 metres; Witton and Habib 2010) and, notably, appear to have engaged in soaring flight
5 (Witton and Habib 2010). It seems probable that extinct species used soaring as a means for
6 scavenging (Witton 2013).

7 While soaring is perhaps the only viable means of locomotion that allows for an obligate,
8 scavenging life-style (Ruxton and Houston 2004b), powered flight is still an efficient means of
9 locomotion. Certainly, avian flight is cheaper than either walking or running (Tucker 1975).
10 We know that many extant birds exist as facultative scavengers because storks, raptors and
11 corvids all take substantial quantities of carrion in their diet (Kendall 2013). Similarly we
12 would expect that extinct species would also scavenge in a similar fashion depending on the
13 efficiency of their flight. For example, early birds such as *Archaeopteryx* are predicted to have
14 been poor, relatively inefficient fliers (Nudds and Dyke 2010) and so ill-suited to finding
15 carrion.

16 The importance of efficient flying over large areas may explain the lack of scavenging
17 behaviour in bats as they are generally nocturnal, a time when they would receive no aid from
18 convective air currents (Norberg 2012). That said, *Necromantis* ("death-eater"), a large bat
19 from the middle to late Eocene (56-33.9 Mya) had a robust cranio-mandibular morphology,
20 and is a likely candidate for scavenging behaviour (Weithofer 1887, Hand et al. 2012).

21 Similar to aerial species, aquatic scavengers have a locomotory benefit because water is a
22 medium that is conducive to low-cost movement (Tucker 1975). This has led some
23 researchers to argue for the likelihood of an obligate scavenging fish (Ruxton and Houston
24 2004a, Ruxton and Bailey 2005). Interestingly, style of swimming in fish does not
25 significantly affect the cost of movement (Williams 1999). Though sharks perhaps best
26 resemble the large soaring fliers as they depend on large pectoral fins in order to maintain lift

1 as they swim. Many shark species have large foraging ranges (e.g. the great white sharks
2 *Carcharodon carcharias*; Bruce et al. 2006) and it seems reasonable that they would use
3 oceanographic currents to further reduce movement costs (Ruxton and Houston 2004a). In
4 fact, facultative scavenging is seen in many selachian groups, including species of extant
5 sharks like white sharks (known to feed on whale carcasses; Fallows et al. 2013), Greenland
6 sharks (feeding on seals; Watanabe et al. 2012), and sixgill sharks (Anderson and Bell 2016).
7 The former which grow up to 6 metres long, can be sustained by 30 kg of whale blubber for
8 over six weeks (Carey et al. 1982). There is evidence too of scavenging in extinct species,
9 where shark teeth have been found in the remains of dinosaurs, mosasaurs and Pliocene
10 mysticete whales (5.3-3.6 Mya; Schwimmer et al. 1997, Ehret et al. 2009).

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

23 Terrestrial environments are the most energetically costly in which to move, which may be
24 due to the low muscular efficiency of running (Tucker 1975) as well as the relative inefficiency
25 of gas exchange in the case of terrestrial mammals (cf. birds and fish Williams 1999).
26 However, the evolutionary transition in posture from the sprawling gait of reptiles to the erect

1 posture of mammals has often been supposed as conferring a huge advantage to the latter.
2 The purported advantages include benefits in terms of speed, efficiency, muscle effort and
3 manoeuvrability (Sullivan 2015). Despite being intuitive, Sullivan (2015) states most of the
4 hypotheses in favour of this idea remain to be tested in the context of archosaur evolution.
5 Metabolic rate however, unquestionably impacts terrestrial species whereby ectotherms such
6 as many modern reptiles, cannot move for sustained periods (Bennett and Ruben 1979). This
7 is exacerbated by their sprawling gait which results in the phenomenon known as Carrier's
8 constraint such that the animal can't move and breathe at the same time because the lateral
9 movements impedes its lungs (Carrier 1987). This would also have been true of extinct
10 species with the same physiology. It is with the evolution of endothermy in the
11 therapsid-mammal lineage (Clarke and Pörtner 2010) that terrestrial vertebrates would have
12 gained the ability to range more widely, a vital component in seeking out carrion. Although
13 the earliest evidence of vertebrate scavenging comes from the Permian (298.9 - 252.17 Mya)
14 where a temnospondyl amphibian fed on the carcass of *Varanops*, a predatory synapsid of the
15 time (Reisz and Tsuji 2006).

16 Modern endothermic mammals can sustain longer periods of energetically expensive
17 activity (Bennett and Ruben 1979) resulting in larger foraging ranges. Today, terrestrial
18 scavenging in the mammals is probably best known in an African context where hyenas,
19 jackals and lions all take sizeable proportions of carrion in their diet. In the spotted hyena
20 (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*) and brown hyena (*Hyaena brunnea*) it can
21 be over 90% (Jones et al. 2015). And although no contemporary terrestrial vertebrate exists
22 as an obligate scavenger, most, if not all, are facultative to some extent (Beasley et al.
23 2015). The particular reliance of hyenas on carrion means we can use them as examples of
24 efficient terrestrial scavengers to compare with other forms. In terms of locomotion, they
25 employ a characteristic "rocking horse gait" which allows them to cover great distances
26 efficiently, loping at 10 km/hr (Mills 1989, Jones et al. 2015). Such long-distance travel is

1 apparent in African wild dogs (*Lycaon pictus*) and many other canids (Pennycuick 1995,
2 Janis and Figueirido 2014). In contrast, big cats like leopards (*Panthera pardus*) rely on
3 ambush (Pennycuick 1995). This allows us to make a broad distinction between the ambush
4 strategies of cats-like forms and the pursuit/ pounce strategies of more dog-like forms, the
5 latter being more suited to scavenging (Janis and Figueirido 2014). These insights allow us
6 to compare extant terrestrial species to their prehistoric forebears given the dominance of
7 mammalian carnivores since the Eocene (56-33.9 Mya) where the order split into the
8 Caniforma and Feliforma (Van Valkenburgh 1987). To take one example, Anyonge (1996)
9 found that *Nimravides*, a genus of sabretooth cat from the Miocene (10.3 to 5.3 Mya), were
10 likely to have been ambush predators which would argue against them taking a lot of carrion.

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

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

vertebrates such as 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 vultures, the genus *Gyps* consists of highly social and colonially nesting species (Fernández-Bellón et al. 2015). These behaviours allow them to forage far more efficiently because one bird can scrounge information on the location of food from another successful forager (Kane et al. 2014). This efficiency has been exploited by mammals such as hyenas who are known to follow groups of vultures (Jones et al. 2015).

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 attuned sense of smell is obviously useful in detecting decaying carrion from the air over a heavily forested habitat.

In contrast to the air, aquatic species have to contend with a low-light environment where visual detection distances are far lower (< 100 m) than they would be in the air. As such, aquatic animals detect resources through chemo- and mechanoreception more so than through vision (Ruxton and Houston 2004a). This is particularly relevant to 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 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.

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 estimated 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) which would have been powerful enough to break open skeletal material
14 (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 (Kane et al. 2016).

21 In their work, the authors demonstrated that species of *intermediate* body masses would
22 have gained the most benefit from scavenging (Kane et al. 2016). This was the result of gut
23 capacity limitations and the effects of competition at the carcass. At the larger extreme this
24 owes to the fact that gut capacity doesn't scale isometrically with body mass so the benefits
25 of greater mass level off; there's only so much food an individual can consume at a single
26 sitting (Calder 1996). For the smaller species, larger competitors would have prevented their

1 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 (*Diomedea*
10 *exulans*), cinereous vultures (*Aegypius monachus*) and condors (*Vultur gryphus*, *Gymnogyps*
11 *californianus*) who all have body masses that can exceed 10 kg and represent some of the
12 heaviest bird species capable of flight (Weimerskirch 1992, Ferguson-Lees and Christie 2001,
13 Donázar et al. 2002). Additionally, as we have noted the Azhdarchid pterosaurs were far
14 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 Azhdarchids existing as *obligate* scavengers, their
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 these pterosaurs behaved similarly. Witton (2013) makes the case that the istiodactyl
21 pterosaurs were the most likely scavengers of this group. The mix of strong and weak
22 features in their skull morphology is indicative of animals that were suited to removing large
23 amounts of flesh from an immobile foodstuff (Witton 2013).

24 Certainly, scavenging should be particularly attractive to flying species compared to
25 mammals. The latter can kill prey up to the same body mass as themselves and sometimes
26 an order of magnitude heavier (e.g. socially hunting lions; Owen-Smith and Mills 2008). In

1 contrast, birds of prey tend to kill prey smaller than themselves (Slagsvold and Sonerud 2007)
2 because of the greater cost of injury and the need to carry off their food. Scavenging
3 provides a means for birds to exploit species that would otherwise be too big for them to kill.

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

14 Because of the random nature of carrion we would expect adaptations that reduce
15 energetic costs of maintenance to be selected for in scavengers as it would maximise the
16 benefit derived from such a sporadic food source. Extant reptiles possess an advantage here,
17 in that over the course of a year their food requirements can be 30 times lower than an
18 endotherm of equal size (Nagy 2005). DeVault and Krochmal (2002) suggest this is an
19 avenue for scavenging in snakes because they "exhibit exceedingly low maintenance
20 metabolisms, and most can survive on a few scant feedings per year. It is, therefore, possible
21 for snakes to rely largely on infrequent, less energy-rich meals." In the same review the
22 authors found occurrences of scavenging spread across five families of snakes and stated that
23 this behaviour is "far more common than currently acknowledged." (DeVault and Krochmal
24 2002). The same reasoning can be applied to crocodiles and their allies (Forrest 2003)
25 because a sit and wait strategy is viable for an ectotherm.

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

1 maximizers relative to toxification minimizers in competitive interactions for carcasses."
2 appears sound, the fact remains that overcoming microorganism toxins is still a beneficial
3 adaptation to any scavenger. Avian scavengers have evolved incredibly acidic stomachs that
4 allow them to consume and process putrefied flesh with no ill effects (Houston and Cooper
5 1975, Roggenbuck et al. 2014). This adaptation is not restricted to vultures though,
6 Grémillet et al. (2012) showed wandering albatrosses (*Diomedea exulans*; so-called "vultures
7 of the seas") had an average pH of 1.5, which enables them to consume fisheries discards
8 and squid carcasses. There is also evidence of selection for "toxification minimizers" beyond
9 birds among the ectotherms. From our earlier arguments we know that ectotherms are
10 limited in their ability to find carrion as quickly as endotherms. This implies later arrivers
11 would benefit especially from well-developed detoxifying apparatus. Shivik (2006) suggests
12 that "specialized oral structures in snakes may have evolved under pressures associated with
13 scavenging." Moreover, some researchers have suggested an evolutionary course from basal
14 fossorial snakes to modern terrestrial species by way of an obligate scavenger intermediate
15 (Bauchot 2006).

16 Conversely, entire clades appear to lack many, if not all, of these phenotypic adaptations.
17 For example, the extant bats appear to lack most of the features we have identified as
18 important in reducing handling time. The larger forms (which are better suited for
19 scavenging, following our previous arguments) are typically frugivores and therefore lack the
20 adaptations for digesting meat. While the smaller carnivorous bats are mainly found in the
21 microbats which are insectivorous (Aguirre et al. 2003). Additionally, their poor terrestrial
22 ability and cost of movement on the ground would also count against them when feeding at a
23 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 scavenging tendency. Ruxton and Houston (2004b) suggest a system with a productivity similar to the Serengeti could have supported a mammalian or reptilian terrestrial scavenger. 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 that 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 as well because of this skewed body mass distribution of herbivores towards larger sizes (O’Gorman and Hone 2012). When we couple this with the fact that skeletal mass scales greater than linearly with body mass (Prange et al. 1979) there would have been a lot of bone material to consume in the environment provided an animal had the biology to process it (Chure and Fiorillo 1997).

Frequently, the interplay between abiotic and biotic factors can impact the ability of an animal to scavenge. We know 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. One result 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. Nocturnal behaviour in the hyaenidae in general has been put forth as an adaptation to reduce competition with these

1 exclusively diurnal birds (Gittleman 2013). If we apply this line of reasoning over evolutionary
2 time-scales, the absence of flying vertebrates in the Palaeozoic may have permitted terrestrial
3 forms to take in a higher proportion of carrion in their diet.

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

11 Staying in the aquatic setting, the phenomenon of occasional bounties of carrion in the
12 form of whale falls has led some researchers to investigate if a scavenger could survive by
13 seeking out these remains exclusively. Ruxton and Bailey (2005) argued that although this is
14 energetically feasible it's ecologically unlikely. Any animal that could find such whale
15 carcasses is unlikely to have ignored other types of carrion. Although no aquatic species have
16 ever exceeded the size of whales, some enormous animals have evolved in this environment
17 before the evolution of cetaceans, including *Leedsichthys*, a bony fish from the Middle
18 Jurassic (174.1-163.5 Mya) and the aquatic Mesozoic reptiles, the plesiosaurs, pliosaurs and
19 ichthyosaurs, that could all exceed 15 metres in length (Ruxton 2011). So, despite being
20 unlikely, the energetic feasibility of a marine scavenger that specialises on large carcasses has
21 a long history. One point of interest is that of the whaling industry, which provided a
22 bonanza of floating carcasses especially during the 20th century (Whitehead and Reeves
23 2005). This meant killer whales could switch from hunting to scavenging, a switch made that
24 much easier by the noise of the whaling vessels that would effectively ring the "dinner-bells"
25 (Whitehead and Reeves 2005).

26 Perhaps the greatest environmental driver of scavenging tendency is that of temperature.

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

15 Conclusion

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

1 feeding ecologies.

2 **Appendix**

3 Scaling relationships for sustainable travel speed are $1.15 \times \text{body mass (kg)}^{0.12}$ and $0.23 \times$
4 $\text{body mass (kg)}^{0.12}$ for mammals and reptiles respectively (Ruxton and Houston 2004b).

5 These are fed into the foraging model $\frac{\text{duration} \times \text{speed}}{2} / 1000$ (Enstipp et al. 2006).

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References

- Aguirre, L. et al. 2003. The implications of food hardness for diet in bats. – *Functional Ecology* 17: 201–212.
- Alexander, R. 2004. Bipedal animals, and their differences from humans. – *Journal of anatomy* 204: 321–330.
- Anderson, G. S. and Bell, L. S. 2016. Impact of marine submergence and season on faunal colonization and decomposition of pig carcasses in the salish sea. – *PloS one* 11: e0149107.
- Anyonge, W. 1996. Locomotor behaviour in plio-pleistocene sabre-tooth cats: a biomechanical analysis. – *Journal of Zoology* 238: 395–413.
- Bates, K. and Falkingham, P. 2012. Estimating maximum bite performance in *Tyrannosaurus rex* using multi-body dynamics. – *Biology Letters* 8: 660–664.
- Bauchot, R. 2006. Snakes: a natural history. – Sterling Publishing Company, Inc.
- Beasley, J. et al. 2015. Ecological role of vertebrate scavengers. – In: Benbow, M. E. et al. (eds.), *Introduction to Carrion Ecology, Evolution, and Their Applications*, chap. 6. CRC Press, Boca Raton, Florida, USA, pp. 107–128.
- Bennett, A. F. and Ruben, J. A. 1979. Endothermy and activity in vertebrates. – *Science* 206: 649–654.
- Blasco, R. et al. 2014. Breaking bones to obtain marrow: A comparative study between percussion by batting bone on an anvil and hammerstone percussion. – *Archaeometry* 56: 1085–1104.
- Brown, C. J. 1989. A study of the Bearded Vulture *Gypaetus barbatus* in southern Africa. Ph.D. thesis, University of Natal (Pietermaritzburg).
- Bruce, B. et al. 2006. Movements and swimming behaviour of white sharks (*carcharodon carcharias*) in australian waters. – *Marine Biology* 150: 161–172.

- 1 Calder, W. A. 1996. Size, function, and life history. – Courier Dover Publications.
- 2 Carbone, C. et al. 2011. Intra-guild competition and its implications for one of the biggest
3 terrestrial predators, *Tyrannosaurus rex*. – Proceedings of the Royal Society B: Biological
4 Sciences 278: 2682–2690.
- 5 Carey, F. G. et al. 1982. Temperature and activities of a white shark, *carcharodon carcharias*. –
6 Copeia : 254–260.
- 7 Carrier, D. R. 1987. The evolution of locomotor stamina in tetrapods: circumventing a mechanical
8 constraint. – Paleobiology : 326–341.
- 9 Chiappe, L. M. and Dyke, G. J. 2006. The early evolutionary history of birds. – Journal of the
10 Palaeontological Society OF Korea 22: 133–151.
- 11 Chin, K. et al. 1998. A king-sized theropod coprolite. – Nature 393: 680–682.
- 12 Chure, D. and Fiorillo, A. 1997. One big al to go and hold the mayo: evidence of scavenging of a
13 specimen of allosaurus from the morrison formation (late jurassic) of wyoming. – Journal of
14 Vertebrate Paleontology 17: 38A.
- 15 Clarke, A. and Pörtner, H.-O. 2010. Temperature, metabolic power and the evolution of
16 endothermy. – Biological Reviews 85: 703–727.
- 17 Collins, M. et al. 2005. Trends in body size across an environmental gradient: a differential
18 response in scavenging and non-scavenging demersal deep-sea fish. – Proceedings of the Royal
19 Society of London B: Biological Sciences 272: 2051–2057.
- 20 Croxall, J. P. and Prince, P. A. 1994. Dead or alive, night or day: how do albatrosses catch squid?
21 – Antarctic Science 6: 155–162.
- 22 DePalma, R. A. et al. 2013. Physical evidence of predatory behavior in *Tyrannosaurus rex*. –
23 Proceedings of the National Academy of Sciences 110: 12560–12564.

- 1 DeVault, T. L. and Krochmal, A. R. 2002. Scavenging by snakes: an examination of the literature.
2 – *Herpetologica* 58: 429–436.
- 3 DeVault, T. L. et al. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary
4 perspectives on an important energy transfer pathway in terrestrial ecosystems. – *Oikos* 102:
5 225–234.
- 6 Domínguez-Rodrigo, M. 2002. Hunting and scavenging by early humans: the state of the debate. –
7 *Journal of World Prehistory* 16: 1–54.
- 8 Donázar, J. A. et al. 2002. Effects of forestry and other land-use practices on the conservation of
9 cinereous vultures. – *Ecological Applications* 12: 1445–1456.
- 10 Ehret, D. J. et al. 2009. Caught in the act: trophic interactions between a 4-million-year-old white
11 shark (*carcharodon*) and mysticete whale from peru. – *Palaios* 24: 329–333.
- 12 Enstipp, M. et al. 2006. Foraging energetics of north sea birds confronted with fluctuating prey
13 availability. – In: Boyd, I. et al. (eds.), *Top Predators in Marine Ecosystems*, chap. 13.
14 Cambridge University Press, Cambridge, UK, pp. 191–210.
- 15 Fahlke, J. M. 2012. Bite marks revisited—evidence for middle-to-late eocene *basilosaurus* isis
16 predation on *dorudon atrox* (both cetacea, *basilosauridae*). – *Palaeontologia Electronica* 15: 32A.
- 17 Fallows, C. et al. 2013. White sharks (*carcharodon carcharias*) scavenging on whales and its
18 potential role in further shaping the ecology of an apex predator. – *PloS one* 8: e60797.
- 19 Farlow, J. and Brinkman, D. 1994. Wear surfaces on the teeth of tyrannosaurs. In: *Dino Fest;*
20 *Proceedings of a Conference for the General Public*. Palaeontological Society Special
21 Publications, vol. 7. pp. 165–175.
- 22 Farlow, J. O. 1994. Speculations about the carrion-locating ability of tyrannosaurs. – *Historical*
23 *Biology* 7: 159–165.
- 24 Ferguson-Lees, J. and Christie, D. A. 2001. *Raptors of the world*. – Houghton Mifflin Harcourt.

- 1 Fernández-Bellon, D. et al. 2015. Density-dependent productivity in a colonial vulture at two spatial
2 scales. – Ecology .
- 3 Forrest, R. 2003. Evidence for scavenging by the marine crocodile *metriorhynchus* on the carcass of
4 a plesiosaur. – Proceedings of the Geologists' Association 114: 363–366.
- 5 Gittleman, J. L. 2013. Carnivore behavior, ecology, and evolution. – Springer Science & Business
6 Media.
- 7 Grady, J. M. et al. 2014. Evidence for mesothermy in dinosaurs. – Science 344: 1268–1272.
- 8 Grémillet, D. et al. 2012. Vultures of the seas: hyperacidic stomachs in wandering albatrosses as an
9 adaptation to dispersed food resources, including fishery wastes. – PloS one 7: e37834.
- 10 Hand, S. et al. 2012. *Necromantis weithofer*, 1887, large carnivorous middle and late eocene bats
11 from the french quercy phosphorites: new data and unresolved relationships. – In: Gunnell, G. F.
12 and Simmons, N. B. (eds.), *Evolutionary History of Bats*. Cambridge University Press, pp.
13 210–251.
- 14 Hedenstrom, A. 1993. Migration by soaring or flapping flight in birds: the relative importance of
15 energy cost and speed. – Philosophical Transactions of the Royal Society of London. Series B:
16 Biological Sciences 342: 353–361.
- 17 Hone, D. W. and Rauhut, O. W. 2010. Feeding behaviour and bone utilization by theropod
18 dinosaurs. – Lethaia 43: 232–244.
- 19 Houston, D. 1974. The role of griffon vultures *gyps africanus* and *gyps ruppellii* as scavengers. –
20 Journal of Zoology 172: 35–46.
- 21 Houston, D. C. 1986. Scavenging efficiency of turkey vultures in tropical forest. – The Condor 88:
22 318–323.
- 23 Houston, D. C. and Cooper, J. 1975. The digestive tract of the whiteback griffon vulture and its
24 role in disease transmission among wild ungulates. – Journal of Wildlife Diseases 11: 306–313.

- 1 Jackson, A. L. et al. 2008. The effect of social facilitation on foraging success in vultures: a
2 modelling study. – *Biology Letters* 4: 311–313.
- 3 Janis, C. M. and Figueirido, B. 2014. Forelimb anatomy and the discrimination of the predatory
4 behavior of carnivorous mammals: The thylacine as a case study. – *Journal of morphology* 275:
5 1321–1338.
- 6 Jarvis, E. D. et al. 2014. Whole-genome analyses resolve early branches in the tree of life of modern
7 birds. – *Science* 346: 1320–1331.
- 8 Jeschke, J. M. et al. 2002. Predator functional responses: discriminating between handling and
9 digesting prey. – *Ecological Monographs* 72: 95–112.
- 10 Jetz, W. et al. 2012. The global diversity of birds in space and time. – *Nature* 491: 444–448.
- 11 Jones, S. et al. 2015. Ecology of african carrion. – In: Benbow, M. E. et al. (eds.), *Introduction to*
12 *Carrion Ecology, Evolution, and Their Applications*, chap. 6. CRC Press, Boca Raton, Florida,
13 USA, pp. 461–494.
- 14 Kane, A. et al. 2014. Vultures acquire information on carcass location from scavenging eagles. –
15 *Proceedings of the Royal Society of London B: Biological Sciences* 281.
- 16 Kane, A. et al. 2016. Body size as a driver of scavenging in theropod dinosaurs. – *The American*
17 *Naturalist* 187.
- 18 Kendall, C. J. 2013. Alternative strategies in avian scavengers: how subordinate species foil the
19 despotic distribution. – *Behavioral Ecology and Sociobiology* 67: 383–393.
- 20 Koenig, R. 2006. Vulture research soars as the scavengers' numbers decline. – *Science* 312.
- 21 Lisney, T. J. et al. 2013. Comparison of eye morphology and retinal topography in two species of
22 new world vultures (aves: Cathartidae). – *The Anatomical Record* 296: 1954–1970.

- 1 Martín-Serra, A. et al. 2016. In the pursuit of the predatory behavior of borophagines (mammalia,
2 carnivora, canidae): Inferences from forelimb morphology. – *Journal of Mammalian Evolution* :
3 1–13.
- 4 Martyniuk, M. P. 2012. A Field Guide to Mesozoic Birds and Other Winged Dinosaurs. – Pan Aves.
- 5 McNab, B. K. 2009. Resources and energetics determined dinosaur maximal size. – *Proceedings of*
6 *the National Academy of Sciences* 106: 12184–12188.
- 7 Mech, L. D. and Boitani, L. 2010. Wolves: behavior, ecology, and conservation. – University of
8 Chicago Press.
- 9 Mills, M. 1989. The comparative behavioral ecology of hyenas: the importance of diet and food
10 dispersion. – In: *Carnivore behavior, ecology, and evolution*. Springer, pp. 125–142.
- 11 Moleón, M. et al. 2014. Humans and scavengers: The evolution of interactions and ecosystem
12 services. – *BioScience* : biu034.
- 13 Monadjem, A. et al. 2012. Survival and population dynamics of the marabou stork in an isolated
14 population, swaziland. – *PLOS ONE* 7: e46434.
- 15 Mundy, P. J. et al. 1992. The vultures of Africa. – Academic Press London.
- 16 Nagy, K. A. 2005. Field metabolic rate and body size. – *Journal of Experimental Biology* 208:
17 1621–1625.
- 18 Niedzwiedzki, G. et al. 2010. Tetrapod trackways from the early middle devonian period of poland.
19 – *Nature* 463: 43–48.
- 20 Norberg, U. M. 2012. Vertebrate flight: mechanics, physiology, morphology, ecology and evolution,
21 vol. 27. – Springer Science & Business Media.
- 22 Nudds, R. L. and Dyke, G. J. 2010. Narrow primary feather rachises in confuciusornis and
23 archaeopteryx suggest poor flight ability. – *Science* 328: 887–889.

- 1 O'Gorman, E. J. and Hone, D. W. E. 2012. Body size distribution of the dinosaurs. – PLoS ONE 7:
2 e51925.
- 3 Owen-Smith, N. and Mills, M. G. 2008. Predator–prey size relationships in an african large-mammal
4 food web. – Journal of Animal Ecology 77: 173–183.
- 5 Palmqvist, P. et al. 2011. The giant hyena *Pachycrocuta brevirostris*: modelling the bone-cracking
6 behavior of an extinct carnivore. – Quaternary International 243: 61–79.
- 7 Parmenter, R. R. and MacMahon, J. A. 2009. Carrion decomposition and nutrient cycling in a
8 semiarid shrub-steppe ecosystem. – Ecological Monographs 79: 637–661.
- 9 Pawar, S. et al. 2012. Dimensionality of consumer search space drives trophic interaction strengths.
10 – Nature 486: 485–489.
- 11 Pennycuik, C. 1995. Energy costs of locomotion and the concept of "foraging radius". – In:
12 Sinclair, A. R. E. and Norton-Griffiths, M. (eds.), Serengeti: dynamics of an ecosystem, chap. 7.
13 University of Chicago Press, USA, pp. 164–18.
- 14 Pobiner, B. 2008. Paleoecological information in predator tooth marks. – Journal of taphonomy 6:
15 373–397.
- 16 Pobiner, B. L. 2015. New actualistic data on the ecology and energetics of hominin scavenging
17 opportunities. – Journal of human evolution 80: 1–16.
- 18 Prange, H. D. et al. 1979. Scaling of skeletal mass to body mass in birds and mammals. –
19 American Naturalist 113: 103–122.
- 20 Rayfield, E. J. et al. 2001. Cranial design and function in a large theropod dinosaur. – Nature 409:
21 1033–1037.
- 22 Reisz, R. R. and Tsuji, L. A. 2006. An articulated skeleton of *Varanops* with bite marks: the oldest
23 known evidence of scavenging among terrestrial vertebrates. – Journal of Vertebrate Paleontology
24 26: 1021–1023.

- 1 Reymond, L. 1985. Spatial visual acuity of the eagle *aquila audax*: a behavioural, optical and
2 anatomical investigation. – *Vision research* 25: 1477–1491.
- 3 Riskin, D. K. et al. 2006. Terrestrial locomotion of the new zealand short-tailed bat *mystacina*
4 *tuberculata* and the common vampire bat *desmodus rotundus*. – *Journal of Experimental Biology*
5 209: 1725–1736.
- 6 Roggenbuck, M. et al. 2014. The microbiome of new world vultures. – *Nature communications* 5.
- 7 Ruxton, G. D. 2011. Zoology: Why are whales big? – *Nature* 469: 481–481.
- 8 Ruxton, G. D. and Bailey, D. M. 2005. Searching speeds and the energetic feasibility of an obligate
9 whale-scavenging fish. – *Deep Sea Research Part I: Oceanographic Research Papers* 52:
10 1536–1541.
- 11 Ruxton, G. D. and Houston, D. C. 2003. Could *Tyrannosaurus rex* have been a scavenger rather
12 than a predator? an energetics approach. – *Proceedings of the Royal Society of London. Series*
13 *B: Biological Sciences* 270: 731–733.
- 14 Ruxton, G. D. and Houston, D. C. 2004a. Energetic feasibility of an obligate marine scavenger. –
15 *Marine ecology. Progress series* 266: 59–63.
- 16 Ruxton, G. D. and Houston, D. C. 2004b. Obligate vertebrate scavengers must be large soaring
17 fliers. – *Journal of Theoretical Biology* 228: 431–436.
- 18 Ruxton, G. D. et al. 2014. Why fruit rots: theoretical support for janzen's theory of
19 microbe–macrobe competition. – *Proceedings of the Royal Society B: Biological Sciences* 281:
20 20133320.
- 21 Sazima, I. and Strüssmann, C. 1990. Necrofagia em serpentes brasileiras: exemplos e previsões. –
22 *Revista Brasileira de Biologia* 50: 463–468.
- 23 Schubert, B. W. and Ungar, P. S. 2005. Wear facets and enamel spalling in tyrannosaurid
24 dinosaurs. – *Acta Palaeontologica Polonica* 50: 93–99.

- 1 Schwimmer, D. R. et al. 1997. Scavenging by sharks of the genus *squalicorax* in the late cretaceous
2 of north america. – *Palaios* : 71–83.
- 3 Sellwood, B. W. and Valdes, P. J. 2006. Mesozoic climates: General circulation models and the
4 rock record. – *Sedimentary geology* 190: 269–287.
- 5 Shivik, J. A. 2006. Are vultures birds, and do snakes have venom, because of macro-and
6 microscavenger conflict? – *BioScience* 56: 819–823.
- 7 Slagsvold, T. and Sonerud, G. 2007. Prey size and ingestion rate in raptors: importance for sex
8 roles and reversed sexual size dimorphism. – *Journal of Avian Biology* 38: 650–661.
- 9 Spiegel, O. et al. 2013. Factors influencing foraging search efficiency: why do scarce lappet-faced
10 vultures outperform ubiquitous white-backed vultures? – *The American Naturalist* 181:
11 E102–E115.
- 12 Spivey, R. et al. 2014. Analysing the intermittent flapping flight of a manx shearwater, *puffinus*
13 *puffinus*, and its sporadic use of a wave-meandering wing-sailing flight strategy. – *Progress in*
14 *Oceanography* 125: 62–73.
- 15 Sullivan, C. 2015. Evolution of hind limb posture in triassic archosauriforms. – In: Dial, K. et al.
16 (eds.), *Great Transformations in Vertebrate Evolution*, chap. 7. University of Chicago Press, USA,
17 pp. 107–124.
- 18 Tenney, S. 1877. A few words about scavengers. – *The American Naturalist* 11: 129–135.
- 19 Thaxter, C. B. et al. 2012. Seabird foraging ranges as a preliminary tool for identifying candidate
20 marine protected areas. – *Biological Conservation* 156: 53–61.
- 21 Tucker, V. A. 1975. The energetic cost of moving about: Walking and running are extremely
22 inefficient forms of locomotion. much greater efficiency is achieved by birds, fish and bicyclists. –
23 *American Scientist* 63: 413–419.

- 1 Van Valkenburgh, B. 1987. Skeletal indicators of locomotor behavior in living and extinct
2 carnivores. – *Journal of Vertebrate Paleontology* 7: 162–182.
- 3 Van Valkenburgh, B. et al. 2003. Chapter 7: Pack hunting in miocene borophagine dogs: Evidence
4 from craniodental morphology and body size. – *Bulletin of the American Museum of Natural*
5 *History* : 147–162.
- 6 Voigt, C. C. et al. 2012. Terrestrial locomotion imposes high metabolic requirements on bats. –
7 *The Journal of experimental biology* 215: 4340–4344.
- 8 Watanabe, Y. Y. et al. 2012. The slowest fish: swim speed and tail-beat frequency of greenland
9 sharks. – *Journal of Experimental Marine Biology and Ecology* 426: 5–11.
- 10 Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition,
11 reproduction and survival in the wandering albatross. – *Oikos* : 464–473.
- 12 Weishampel, D. B. et al. 2004. *The dinosauria*. – University of California Press.
- 13 Weithofer, A. 1887. Zur kenntniss der fossilen cheiropteren der französischen phosphorite. –
14 *Mathematisch-naturwissenschaftlich* 96: 341—360.
- 15 Whitehead, H. and Reeves, R. 2005. Killer whales and whaling: the scavenging hypothesis. –
16 *Biology Letters* 1: 415–418.
- 17 Williams, T. M. 1999. The evolution of cost efficient swimming in marine mammals: limits to
18 energetic optimization. – *Philosophical Transactions of the Royal Society of London B: Biological*
19 *Sciences* 354: 193–201.
- 20 Witton, M. P. 2013. *Pterosaurs: natural history, evolution, anatomy*. – Princeton University Press,
21 USA.
- 22 Witton, M. P. and Habib, M. B. 2010. On the size and flight diversity of giant pterosaurs, the use
23 of birds as pterosaur analogues and comments on pterosaur flightlessness. – *PLOS ONE* 5:
24 e13982.

- ¹ Witton, M. P. and Naish, D. 2008. A reappraisal of azhdarchid pterosaur functional morphology
- ² and paleoecology. – PLOS ONE 3: e2271.