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4 **The natural history of scavenging in vertebrates**

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Abstract

Scavengers existed in the past and they exist now. Often under appreciated. Three main habitat types considered: land, air and sea. Different drivers in these areas. Review looks at these

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

The Difficulty of Scavenging

The chief hurdle to scavenging is finding a sufficient quantity of food, the occurrence of which is difficult to predict in space and time. Once found, the scavenger has to then overcome the agents of decay produced by the action of microorganisms on the carcass (Ruxton et al. 2014). The idea of scrounging from predator kills is undermined by studies showing that in the majority of ecosystems more animals die from disease and starvation than predation (Benbow et al. 2015). Thus, any animal existing as a scavenger must maximise its detection capabilities and minimise its locomotory costs (Ruxton and Houston 2004b). The habitat must also be productive enough to sustain an animal biomass that will eventually produce carcasses.

Aerial Scavengers

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

Vultures represent the best known scavengers on Earth. These birds consist of two convergent groups, from the old and the new world and represent the only example of obligate vertebrate scavengers today. The families from which modern vultures arose, the Accipitridae and Cathartidae, appear during the Palaeocene (66 - 56 Mya) (Jetz et al. 2012, Jarvis et al. 2014). Given their unique position, they have been extensively studied to

1 determine what adaptations they possess that allows them to so flourish in this niche.

2 Underscoring their prowess are studies such as Ogada et al. (2012) who note a three fold
3 increase in carcass persistence times in the absence of vultures. As such, we can begin by
4 exploring the adaptations and the environments of vultures to draw comparisons with other
5 scavenging species and *their* environments.

6 Species capable of flight have effectively added an extra spatial dimension, i.e. the
7 vertical component, to their sensory environment over land animals. This allows them to look
8 down on a landscape where they are unencumbered by obstacles that would obstruct the view
9 of a terrestrial scavenger. Such an ability has obvious benefits in detecting carrion. Vultures
10 are known to have impressive visual acuity with one estimate indicating Lappet-faced
11 Vultures (*Torgos tracheliotus*) are capable of detecting a 2 metre carcass over 10 km away
12 (Spiegel et al. 2013). We know that many birds exist as facultative scavengers; storks, eagles,
13 corvids, are all known to take substantial quantities of carrion in their diet. And eagles in
14 particular are known to have highly developed visual abilities. It follows from this that the
15 evolution of flight allowed aerial animals to detect far more carrion than their terrestrial
16 counterparts (Lisney et al. 2013).

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

23 Aside from sight, three species within the new world family Cathartidae, (genus
24 *Cathartes*), have well developed olfactory systems (Lisney et al. 2013). Among them are the
25 Turkey Vultures (*Cathartes aura*) which were able to locate 90% of baits set out in a tropical
26 forest (Houston 1986). This would be impossible for the visually reliant old world species.

1 This point illustrates how the environment can impact search efficiency depending on the
2 sensory system that's used.

3 Flight is also a cheaper means of locomotion than running (Tucker 1975). This advantage
4 can be extended further in larger species by engaging in soaring instead of flapping flight,
5 which is even cheaper still (approximately twice BMR) (Hedenstrom 1993). The benefits this
6 confers are clear from the information we have on the enormous foraging ranges of many
7 vultures (Spiegel et al. 2013). Clearly, it would be pointless to have incredible detection
8 abilities and not have a cost efficient movement to benefit from it. Although, as with
9 detection ability, the environment has a role to play here. Vultures and eagles tend to soar
10 using thermals and if these air pockets don't form, say on a cloudy day, the bird is grounded
11 (Mundy et al. 1992). In many habitats (e.g. the arctic) it is simply not possible for
12 sufficiently powerful thermals to form and as a consequence large-bodied vultures cannot
13 exist. The upshot of this is that terrestrial carnivores like bears and wolves take more carrion
14 (DeVault et al. 2003).

15 Avian flight originates in the Late Jurassic (163.5-145 Million years ago - Mya),
16 coincident with the fossils of *Archaeopteryx lithographica* so many of these benefits would
17 have been realised from that point on for carnivorous birds. However, vertebrate flight is
18 much older than this where pterosaurs predate bird origins by a considerable margin in the
19 Late Triassic (235-201.3 Mya). Scavenging in this diverse group has been hypothesised many
20 times before. Certain clades of these animals could reach enormous sizes (e.g. Azhdarchids
21 with wingspans of 11 metres (Witton and Habib 2010)) and look to have engaged in soaring
22 flight (Witton and Habib 2010). Although Witton and Naish (2008) argued that neck
23 inflexibility and straight, rather than hooked jaw morphology points against their existing as
24 *obligate* scavengers, Azhdarchid terrestrial proficiency indicates they would have been
25 comfortable foraging on the ground. Indeed, extant Marabou Storks (*Leptoptilos crumenifer*)
26 have a comparable morphology and are noted facultative scavengers so it is reasonable to

1 believe that certain pterosaurs behaved similarly.

2 Large body size confers substantial dominance and starvation resistance benefits (Ruxton
3 and Houston 2004b). Thus, we would expect scavengers to have this trait selected for even
4 in the case of weight-constrained fliers. Cinereous Vultures (*Aegypius monachus*) and condors
5 (*Vultur gryphus*, *Gymnogyps californianus*) all have body masses that can exceed 10 kg and
6 represent some of the heaviest bird species capable of flight (Ferguson-Lees and Christie
7 2001, Donázar et al. 2002). And as we have noted the Azhdarchid pterosaurs were far bigger
8 again, with estimated body masses of over 200 kg (Witton and Habib 2010).

9 The only other vertebrate group capable of powered flight are the bats where scavenging
10 has not been recorded to our knowledge. Their visual acuity is famously poor and
11 echolocation would not lend itself to discovering immobile carrion. Their small size and poor
12 terrestrial ability would also count against them at a carcass (Riskin et al. 2006). The bat
13 fossil record is notoriously poor owing to their fragile skeletons so we are unable to determine
14 if extinct species were more suited to this lifestyle (Eiting and Gunnell 2009).

15 **Terrestrial Scavengers**

16 A simplification of terrestrial, vertebrate scavengers is one of them existing in a
17 two-dimensional plane while foraging for carrion directly. They can detect carcasses at a
18 range that is defined by the radius of their sensory organs, usually the visual and olfactory
19 senses. As a consequence, they have a much more restricted view of the landscape than do
20 aerial foragers. No contemporary terrestrial vertebrate exists as an obligate scavenger but
21 most if not all are facultative scavengers to some extent (Beasley et al. 2015). Ruxton and
22 Houston (2004b) offer a reason for this in that the traits that allow for vultures to exist as
23 scavengers undermined their ability to hunt but that the same forces have not prevented
24 mammals from doing so. Interestingly, the same authors calculated that "a 1 tonne mammal

1 or reptile, in an ecosystem yielding carrion at densities similar to the current Serengeti, could
2 have met its energy requirements if it could detect carrion over a distance of the order of
3 400–500 m."(Ruxton and Houston 2004b).

4 Terrestrial scavenging in the mammals is probably best known in an African context
5 where hyenas, jackals and lions all take sizable proportions of carrion in their diet. In the
6 spotted hyena (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*) and brown hyena (*Hyaena*
7 *brunnea*) it can be over 90% (Jones et al. 2015). Therefore, we can again use these species
8 as our efficient terrestrial scavengers to compare with other forms.

9 Similar to vultures they have well developed sensory organs, whereby they can smell a
10 rotting carcass 4 km away and can hear the vocalisations of conspecifics at a distance of 10
11 km (Mills 1989). They have a characteristic "rocking horse gait" which allows them to cover
12 great distances efficiently (Jones et al. 2015). A major difficulty for terrestrial scavengers is
13 competition with vultures. Nocturnal behaviour in the Hyaenidae in general has been put forth
14 as an adaptation to reduce competition with these exclusively diurnal birds (Gittleman 2013).
15 The bone crushing ability of hyenas reveals another useful scavenger trait. Since carrion is
16 not dispatched directly, often the most easily accessible and choicest components of the
17 carcass will be missing or, if present, will be fought over. Being able to extract nutrients from
18 remnants gives the scavenger a great advantage. Osteophagy is known across a range of
19 terrestrial carnivores and given some fat-rich mammalian bones have an energy density (6.7
20 kJ/g) comparable with that of muscle tissue, it makes skeletal remains an enticing resource
21 (Brown 1989). This ability reached its zenith among hyenas with the evolution of the 110 kg
22 *Pachycrocuta brevirostris* during the Pliocene (Palmqvist et al. 2011). Some work on extinct
23 sabretooths suggests they may have left a large amount of food for would-be scavengers
24 because of their unique skull morphology. As a result, the decline of Machairodontinae
25 sabretooths has been offered as an explanation for the extinction of *P brevirostris* (Palmqvist
26 et al. 2011).

1 The order Carnivora sees its origins in the Middle Eocene (56-33.9 Mya) where it split
2 into the Caniforma and Feliforma. And many of the aforesaid adaptations for scavenging are
3 found in these other major terrestrial mammalian carnivores. Though the specific mix of
4 features realised in hyenas suggest this is the model organism for terrestrial scavenging
5 among mammals in the past. For example, the bone-crushing dogs that evolved during the
6 Oligocene (subfamily Borophaginae) have been compared to hyenas in terms of their feeding
7 ecology (Van Valkenburgh et al. 2003, Martín-Serra et al. 2016). Certainly, it is profitable to
8 compare extant terrestrial species to their prehistoric forebears given the dominance of
9 mammalian carnivores since the Eocene.

10 Interestingly such comparisons have given insight into the feeding ecology of early
11 hominins who, for instance, had the ability to craft tools for breaking open bones (Blasco
12 et al. 2014). The question of where our ancestors placed on the hunter-scavenger axis during
13 the Plio-Pleistocene has been a matter of debate for years. A recent study investigating
14 potential scavenging opportunities for hominins in Kenya found that, even when discounting
15 bone material, there is a substantial amount of scavengeable meat left on predated remains;
16 sufficient to sustain the requirements of an adult male *Homo erectus* (Pobiner 2015). In
17 some historical hominin-inhabited areas there were a greater number of felids than hyenids.
18 This is significant because hyenas are likely to have left far less flesh on a carcass than a felid
19 such as a sabretooth enabling contemporaneous hominins to benefit (Pobiner 2015). The
20 intelligence, resultant tool-use and cooperative nature of hominins meant they could likely
21 adapt to take on more or less carrion depending on their environment (Moleón et al. 2014).

22 By contrast to mammals, a successful reptilian scavenger requires a far different set of
23 adaptations. Modern forms are ectothermic, limiting their activity periods. This is exacerbated
24 by the sprawling gait seen in many lizards which results in Carrier's Constraint such that the
25 animal can't move and breathe at the same time because the lateral movements impedes its
26 lungs (Carrier 1987). This manifests itself in aspects such as maximum sustainable speed

1 where an equivalent mammal has a six to seven fold increase (Ruben 1995). A lower
2 metabolism does give reptiles an advantage however, in that over the course of a year their
3 food requirements can be 30 times smaller than an endotherm of equal size (Nagy 2005).
4 Any adaptations that reduce energetic costs are likely to be selected in scavengers. DeVault
5 and Krochmal (2002) suggest this is an avenue for scavenging in snakes because they
6 "exhibit exceedingly low maintenance metabolisms, and most can survive on a few scant
7 feedings per year. It is, therefore, possible for snakes to rely largely on infrequent, less
8 energy-rich meals." In the same review the authors found occurrences of scavenging spread
9 across five families of snakes and stated that this behaviour is "far more common than
10 currently acknowledged." (DeVault and Krochmal 2002). The same reasoning can be applied
11 to crocodiles and their allies (Forrest 2003).

12 Unsurprisingly, given their enduring appeal, the prevalence of scavenging has been
13 explored in the carnivorous, theropod dinosaurs. These animals ranged from the chicken-sized
14 to the whale-sized all of which were bipedal. They are quite alien to anything we know today
15 which restricts our ability to understand their ecology far more so than extinct mammals
16 (Weishampel et al. 2004). Of relevance, are the questions that still persist about their
17 metabolism (Grady et al. 2014) and sensory perception (Farlow 1994). We do know that they
18 walked with the erect gait of mammals or birds rather than the sprawling gait of lizards and
19 that they were most likely facultative scavengers (Weishampel et al. 2004, DePalma et al.
20 2013). Much work has focused on the existence of the behaviour in *Tyrannosaurus rex*
21 (Ruxton and Houston 2003, Carbone et al. 2011) but a recent energetics study investigated
22 the likely prevalence of scavenging across a range of body sizes. In it the authors
23 demonstrated that species of intermediate body masses (approx. 500 kg) would have gained
24 the most benefit from scavenging. This was the result of gut capacity limitations and the
25 effects of competition at the carcass. At the larger extreme this owes to the fact that gut
26 capacity doesn't scale isometrically with body mass so the benefits of greater mass level off;

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

3 As we discussed for the case of Cenozoic carnivores, osteophagy could be extremely
4 beneficial to a scavenger. In Mesozoic systems some extremely large theropod dinosaurs had
5 a morphology which suggests an ability to process bone e.g. the robust skull and dentition of
6 *T. rex* (Hone and Rauhut 2010). There is direct evidence that *T. rex* did this in the form of
7 distinctive wear marks on its tooth apices (Farlow and Brinkman 1994, Schubert and Ungar
8 2005) and the presence of bone fragments in its coprolites (Chin et al. 1998). The animal
9 also had an enormous bite force, with one estimate putting it at 57000 Newtons (Bates and
10 Falkingham 2012). This is noted as being powerful enough to break open skeletal material
11 (Rayfield et al. 2001). Osteophagy may have been even more viable during this era because
12 the body mass distribution of herbivores tended to be skewed towards larger sizes (O'Gorman
13 and Hone 2012). When we couple this with the fact that skeletal mass scales greater than
14 linearly with body mass (Prange et al. 1979) there would have been a lot of bone material to
15 consume in the environment provided an animal had the biology to process it (Chure and
16 Fiorillo 1997).

17 Of course, tetrapod terrestrial dominance predates the evolution of the dinosaurs. It is in
18 the Permian, almost 300 millions years ago, that we have the earliest evidence of vertebrate
19 scavenging where a temnospondyl amphibian fed on the carcass of *Varanops*, a predatory
20 synapsid of the time (Reisz and Tsuji 2006). The absence of flying vertebrates in the
21 Palaeozoic may have permitted terrestrial forms to take in a higher proportion of carrion in
22 their diet. As noted earlier, a system similar to the Serengeti in productivity could have
23 supported a terrestrial scavenger (Ruxton and Houston 2004b). Indeed, in systems that were
24 dominated by large ectothermic or mesothermic vertebrates the same primary productivity
25 would have supported a greater biomass (McNab 2009). The upshot of this is there was a
26 higher biomass of herbivores dying and offering scavenging opportunities. Predators were

1 large bodied too compared to extant mammalian predators (McNab 2009), and so, especially
2 if they were ectothermic, could last longer between meals rendering scavenging a more
3 attractive behaviour relative to predation.

4 **Aquatic Scavengers**

5 Primary productivity is lower in almost all aquatic systems than terrestrial systems (except
6 deserts) so as we go up the food chain the density of carcasses worth scavenging is going to
7 be lower. But it is certainly known to occur in many aquatic vertebrates. An aquatic
8 environment presents challenges for direct observational studies and so, similar to the
9 approaches involving extinct species, much work has approached the question of scavenging
10 propensity from an energetics perspective. Although, as with the aerial and terrestrial
11 environments we have evidence of facultative scavenging among aquatic species. For
12 example, the remains of a mosasaur and a terrestrial hadrosaur were discovered with
13 embedded teeth from a Cretaceous shark, *Squalicorax* (Schwimmer et al. 1997). As well as a
14 likely instance of scavenging between a 4-million-year-old white shark (*Carcharodon*) and
15 mysticete whale from Peru (Ehret et al. 2009). The existence of an obligate scavenger in a
16 marine setting is uncertain (Britton and Morton 1994, Smith and Baco 2003, Ruxton and
17 Houston 2004a, Ruxton and Bailey 2005). Depending on the species, a carcass in this
18 environment either floats or descends to the sea floor (Whitehead and Reeves 2005). In the
19 latter low-light environment, visual detection distances are far lower (< 100 m) than they
20 would be in the air. As such, animals detect resources through chemo- and mechanoreception
21 more so than through vision (Ruxton and Houston 2004a). However, water is a medium that
22 is conducive to low-cost movement (Tucker 1975) and so may be able to support an obligate
23 scavenging fish (Ruxton and Houston 2004a, Ruxton and Bailey 2005). Beasley et al. (2015)
24 do note that "some benthic scavengers (e.g., hagfish: family Myxiniidae) rely on necrophagy

1 for a large portion of their diet and may indeed be obligate scavengers".

2 Extant aquatic snakes are deemed as having the most suitable physiology and
3 environment for scavenging. A hypothesis put forth by Sazima and Strüssmann (1990)
4 argued that chemical gradients in water would allow for a relatively easier detection of
5 carrion. This gained some support from DeVault and Krochmal (2002), who found a
6 preponderance of aquatic snake species in their review of this behaviour.

7 The presence of occasional bounties of carrion in the form of whale falls has led some
8 researchers to investigate if a scavenger could survive by seeking out these remains
9 exclusively. Ruxton and Bailey (2005) argued that although this is energetically feasible it's
10 ecologically unlikely. Any animal that could seek out such whale carcasses is unlikely to have
11 ignored other types of carrion. Although no aquatic species have ever exceeded the size of
12 whales, some enormous animals have evolved in this environment before the evolution of
13 whales, including *Leedsichthys*, a bony fish from the Middle Jurassic (174.1-163.5 Mya), that
14 weighed in excess of 20 tonnes. Thus, the energetic feasibility of a marine scavenger has a
15 long history. One point of interest is that of the whaling industry, which provided a bonanza
16 of floating carcasses especially during the 20th century (Whitehead and Reeves 2005). This
17 meant Killer Whales (*Orcinus orca*) could switch from hunting to scavenging, a switch made
18 that much easier by the noise of the whaling vessels that would effectively ring the
19 "dinner-bells" (Whitehead and Reeves 2005). Early whales such as *Basilosaurus* seem to fit
20 into the same niche as Killer Whales and we have some evidence for scavenging in this group
21 as well (Fahlke 2012). A final point to make is that vertebrates are relatively rarer in aquatic
22 environments, because even large animals can get support from the buoyancy of the water
23 without needing a backbone.

Ecological Role

It is recognised that scavengers keep energy flows at a higher trophic level in food webs than decomposers because they consume relatively more carrion (DeVault et al. 2003). They are also hugely important for the dispersal of nutrients (Beasley et al. 2015). Consider the diversity of animals that can end up feeding at the carcass of an elephant. Here we have an incredibly dense and nutrient rich patch that ends up being distributed widely. In the absence of vertebrate scavengers, invertebrates and microorganisms would consume the carcass in-situ or at least distribute the constituent nutrients over a much shorter range. This effect has been magnified as vertebrates evolved certain key traits that allowed them to range farther, namely an upright gait, an endothermic metabolism and of course, flight. To quantify this effect with a simple example we can turn to some allometric relationships relating sustainable travelling speed to body mass. In the case of mammals and reptiles these are $1.15 * \text{body mass (kg)}^{0.12}$ and $0.23 * \text{body mass (kg)}^{0.12}$ respectively (Ruxton and Houston 2004b). We can insert these into a foraging radius model $((\text{duration} * \text{speed})/2)/1000$ for a 12 hour foraging day which shows that while a 10 kg reptile can range 6.5 km an equally sized mammal can range nearly 33 km (Enstipp et al. 2006). Thus, in an ecological context, the evolution of these steps coupled with the ability to scavenge resulted in a world with a far more widely distributed nutrient landscape.

The Role of Climate

The geological record shows the Earth has undergone radical fluctuations in temperature. This will have had a significant bearing on the availability and persistence of carrion. To illustrate the point, a 10°C increase in ambient temperature can double carcass decomposition rates (Parmenter and MacMahon 2009) and geological evidence indicates that the Mesozoic Earth was at least 6°C warmer than now (Sellwood and Valdes 2006). In

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

9 **Acknowledgments**

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