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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" (Benbow 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.

1 **The Difficulty of Scavenging**

2 The chief hurdle to scavenging is finding a sufficient quantity of food, the occurrence of which
3 is difficult to predict in space and time. Once found the scavenger has to overcome the
4 agents of decay produced by the action of microorganisms on the carcass. The idea of
5 scrounging from predator kills is undermined from studies showing that in the majority of
6 ecosystems more animals die from disease and starvation than predation (Benbow et al.
7 2015). Thus, any animal existing as a scavenger must maximise its detection capabilities and
8 minimise its locomotory costs (Ruxton and Houston 2004b). The habitat must also be
9 productive enough to sustain an animal biomass that will eventually produce carcasses.

10 **Aerial Scavengers**

11 Vultures represent the best known scavengers on Earth. These birds consist of two
12 convergent groups, from the old and the new world and represent the only example of
13 obligate vertebrate scavengers today. Given their unique position, they have been extensively
14 studied to determine what adaptations they possess that allows them to so flourish in this
15 niche. As such, we can begin by exploring the adaptations and the environments of vultures
16 to draw comparisons with other scavenging species and *their* environments.

17 Species capable of flight have effectively added an extra spatial dimension, i.e. the
18 vertical component, to their sensory environment over land animals. This allows them to look
19 down on a landscape where they are unencumbered by obstacles that would obstruct the view
20 of a terrestrial scavenger. Such an ability has obvious benefits in detecting carrion. Vultures
21 are known to have impressive visual acuity with one estimate indicating Lappet-faced
22 Vultures (*Torgos tracheliotus*) are capable of detecting a 2 metre carcass over 10 km away
23 (Spiegel et al. 2013). We know that many birds exist as facultative scavengers; storks, eagles,
24 corvids, are all known to take substantial quantities of carrion in their diet. And eagles in

1 particular are known to have highly developed visual abilities. It follows from this that the
2 evolution of flight allowed aerial animals to detect far more carrion than their terrestrial
3 counterparts (Lisney et al. 2013).

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

10 Aside from sight, three species within the new world family Cathartidae, (genus
11 *Cathartes*), have well developed olfactory systems (Lisney et al. 2013). Among them are the
12 Turkey Vultures *Cathartes aura* which were able to locate 90% of baits set out in a tropical
13 forest (Houston 1986). This would be impossible for the visually reliant old world species.
14 This point illustrates how the environment can impact search efficiency depending on the
15 sensory system that's used.

16 Flight is also cheaper means of locomotion than running (Tucker 1975). This advantage
17 can be extended further in larger species by engaging in soaring instead of flapping flight,
18 which is even cheaper still (approximately twice BMR) (Hedenstrom 1993). The advantages
19 this confers are clear from the information we have on the enormous foraging ranges of some
20 seabirds and accipiters (Bamford et al. 2007). Clearly, it would be pointless to have incredible
21 detection abilities and not have a cost efficient movement to benefit from it. Although, as
22 with detection ability, the environment has a role to play here. Vultures and eagles tend to
23 soar using thermals and if these air pockets don't form, say on a cloudy day, the bird is
24 grounded (Mundy et al. 1992). In many habitats (e.g. the arctic) it is simply not possible for
25 sufficiently powerful thermals to form and as a consequence large-bodied vultures cannot
26 exist. The upshot of this is that terrestrial carnivores like bears and wolves take more carrion

1 (DeVault et al. 2003).

2 Avian flight originates in the Jurassic Period, coincident with the fossils of *Archaeopteryx*
3 *lithographica* so many of these benefits would have been realised from that point on for
4 carnivorous birds. However, vertebrate flight is much older than this where pterosaurs predate
5 bird origins by a considerable margin in the Triassic Period. Scavenging in this diverse group
6 has been hypothesised many times before. Certain clades of these animals could reach
7 enormous sizes (e.g. Azhdarchids with wingspans of 11 metres) and look to have engaged in
8 soaring flight (Witton and Habib 2010). Although Witton and Naish (2008) argued that neck
9 inflexibility and straight, rather than hooked jaw morphology points against their existing as
10 *obligate* scavengers, Azhdarchid terrestrial proficiency indicates they would have been
11 comfortable foraging on the ground. Indeed, extant Marabou Storks have a comparable
12 morphology and are noted facultative scavengers so it is reasonable to believe that certain
13 pterosaurs behaved similarly.

14 Large body size confers substantial dominance benefits (Ruxton and Houston 2004b).
15 Thus, we would expect scavengers to have this trait selected for even in the case of
16 weight-constrained fliers. Cinereous Vultures (*Aegypius monachus*) and condors (*Vultur*
17 *gryphus*, *Gymnogyps californianus*) all have body masses that can exceed 10 kg and represent
18 some of the heaviest bird species capable of flight (Ferguson-Lees and Christie 2001, Donázar
19 et al. 2002). And as we have noted the Azhdarchid pterosaurs were far bigger again, with
20 estimated body masses of around 80 kg.

21 The only other vertebrate group capable of powered flight are the bats where scavenging
22 has not been recorded to our knowledge. Their visual acuity is famously poor and
23 echolocation does not lend itself to discovering immobile carrion. Their small size and poor
24 terrestrial ability would also count against them at a carcass. The bat fossil record is
25 notoriously poor owing to their fragile skeletons so we are unable to determine if extinct
26 species were more suited to this lifestyle.

1 Terrestrial Scavengers

2 A simplificaition of terrestrial, vertebrate scavengers is one of them existing in a
3 two-dimensional plane while foraging for carrion directly. They can detect carcasses at a
4 range that is defined by the radius of their sensory organs, usually the visual and olfactory
5 senses. As a consequence, they have a much more restricted view of the landscape than do
6 aerial foragers. No contemporary terrestrial vertebrate exists as an obligate scavenger but
7 most if not all are facultative scavengers to some extent. Ruxton and Houston (2004b) offer
8 a reason for this in that the traits that allow for vultures to exist as scavengers undermined
9 their ability to hunt but that the same forces have not prevented mammals from doing so.
10 The same authors calculated that "a 1 tonne mammal or reptile, in an ecosystem yielding
11 carrion at densities similar to the current Serengeti, could have met its energy requirements if
12 it could detect carrion over a distance of the order of 400–500 m."(Ruxton and Houston
13 2004b).

14 Terrestrial scavenging in the mammals is probably best known in an African context
15 where hyenas, jackals and lions all take sizable proportions of carrion in their diet. In the
16 spotted hyena (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*) and brown hyena (*Hyaena*
17 *brunnea*) it can be as high as 99% (Benbow et al. 2015). Therefore, we can again use these
18 species as our efficient terrestrial scavengers to compare with other forms.

19 Similar to vultures they have well developed sensory organs, particularly in olfaction
20 whereby they can detect a rotting carcass 2 km downwind. They have a characteristic
21 "rocking horse gait" which allows them to cover great distances efficiently. The bone
22 crushing ability of hyenas reveals another useful scavenger trait. Since carrion is not
23 dispatched directly, often the most easily accessible and choicest components of the carcass
24 will be missing or, if present, will be fought over. Being able to extract nutrients from
25 remnants gives the scavenger a great advantage. Osteophagy is known across a range of

1 terrestrial carnivores. Some fat-rich mammalian bones have an energy density (6.7 kJ/g)
2 comparable with that of muscle tissue, making skeletal remains an enticing resource (Brown
3 1989). This ability reached its zenith among hyenas with the evolution of the 110 kg
4 *Pachycrocuta brevirostris* during the Pliocene (Palmqvist et al. 2011). Some work on extinct
5 sabretooths suggests they may have left a large amount of food for would-be scavengers
6 because of their unique skull morphology. As a result the decline of Machairodontinae
7 sabretooths has been offered as an explanation for the extinction of *P brevirostris* (Palmqvist
8 et al. 2011). A major difficulty for terrestrial scavengers is competition with vultures.
9 Nocturnal behaviour in the Hyaenidae in general has been put forth as an adaptation to reduce
10 competition with these exclusively diurnal birds (Gittleman 2013).

11 The order Carnivora sees its origins in the Eocene where it split into the Caniforma and
12 Feliforma. And many of the aforesaid adaptations for scavenging are found in these other
13 major terrestrial mammalian carnivores. Though the specific mix of features realised in
14 hyenas suggest this is the model organism for terrestrial scavenging among mammals in the
15 past. Indeed, the bone-crushing dogs that evolved during the Oligocene (subfamily
16 Borophaginae) have been compared to hyenas in terms of their feeding ecology
17 (Van Valkenburgh et al. 2003, Martín-Serra et al. 2016).

18 Interestingly such comparisons have given insight into the feeding ecology of early
19 hominins who, for instance, had the ability to craft tools for breaking open bones (Hone and
20 Rauhut 2010, Blasco et al. 2014). The question of where our ancestors placed on the
21 hunter-scavenger axis during the Plio-Pleistocene has been a matter of debate for years. A
22 recent study investigating potential scavenging opportunities for hominins in Kenya found
23 that, even when discounting bone material, there is a substantial amount of scavengeable
24 meat left on predated remains; sufficient to sustain the requirements of an adult male *Homo*
25 *erectus* (Pobiner 2015). In some historical hominin-inhabited areas there were a greater
26 number of felids than hyenids. This is significant because hyenas will leave far less flesh on a

1 carcass than a felid such as a sabretooth enabling contemporaneous hominins to benefit
2 (Pobiner 2015). The intelligence, resultant tool-use and cooperative nature of hominins
3 means they could likely adapt to take on more or less carrion depending on their
4 environment.

5 By contrast to mammals, a successful reptilian scavenger requires a far different set of
6 adaptations. Modern forms are ectothermic, limiting their activity periods. This is exacerbated
7 by the sprawling gait seen in lizards which results in Carrier's Constraint such that the animal
8 can't move and breathe at the same time because the lateral movements impedes its lungs
9 (Carrier 1987). This manifests itself in aspects such as maximum sustainable speed where an
10 equivalent mammal has a six to seven fold increase (Ruben 1995). A lower metabolism does
11 give reptiles an advantage however, in that over the course of a year their food requirements
12 can be 30 times smaller than an endotherm of equal size (Nagy 2005). Any adaptations that
13 reduce energetic costs are likely to be selected in scavengers. DeVault and Krochmal (2002)
14 suggest this is an avenue for scavenging in snakes because they "exhibit exceedingly low
15 maintenance metabolisms, and most can survive on a few scant feedings per year. It is,
16 therefore, possible for snakes to rely largely on infrequent, less energy-rich meals." In the
17 same review the authors found occurrences of scavenging spread across five families of snakes
18 and stated that this behaviour is "far more common than currently acknowledged." (DeVault
19 and Krochmal 2002).

20 Unsurprisingly, given their enduring appeal, the prevalence of scavenging has been
21 explored in the carnivorous, theropod dinosaurs. These animals ranged from the chicken-sized
22 to the whale-sized all of which were bipedal. They are quite alien to anything we know today
23 which restricts our ability to understand their ecology far more so than extinct mammals
24 (Weishampel et al. 2004). Of relevance, are the questions that still persist about their
25 metabolism (Grady et al. 2014) and sensory perception. We do know that they walked with
26 the erect gait of mammals or birds rather than the sprawling gait of lizards and that they

1 were most likely facultative scavengers (DePalma et al. 2013). Much work has focused on the
2 existence of the behaviour in *Tyrannosaurus rex* (Ruxton and Houston 2003, Carbone et al.
3 2011) but a recent energetics study investigated the likely prevalence of scavenging across a
4 range of body sizes. In it the authors demonstrated that species of intermediate body masses
5 (approx. 500 kg) would have gained the most benefit from scavenging. This was the result of
6 gut capacity limitations and the effects of competition at the carcass. At the larger extreme
7 this owes to the fact that gut capacity doesn't scale isometrically with body mass so the
8 benefits of greater mass level off; there's only so much food an individual can consume at a
9 single sitting. For the smaller species, larger competitors would have prevented their access to
10 carrion.

11 As we discussed for the case of Cenozoic carnivores, osteophagy could be extremely
12 beneficial to a scavenger. In Mesozoic systems some extremely large theropod dinosaurs had
13 a morphology which suggests an ability to process bone e.g. the robust skull and dentition of
14 *T. rex*. There is direct evidence that *T. rex* did this in the form of distinctive wear marks on
15 its tooth apices (Farlow and Brinkman 1994, Schubert and Ungar 2005) and the presence of
16 bone fragments in its coprolites (Chin et al. 1998). The animal also had an enormous bite
17 force, with one estimate putting it at 57000 Newtons (Bates and Falkingham 2012). This is
18 noted as being powerful enough to break open skeletal material (Rayfield et al. 2001).
19 Osteophagy may have been even more viable during this era because the body mass
20 distribution of herbivores tended to be skewed towards larger sizes (O'Gorman and Hone
21 2012). When we couple this with the fact that skeletal mass scales greater than linearly with
22 body mass (Prange et al. 1979) there would have been a lot of bone material to consume in
23 the environment provided an animal had the biology to process it (Chure and Fiorillo 1997).

24 Of course, tetrapod terrestrial dominance predates the evolution of the dinosaurs. It is in
25 the Permian, almost 300 millions years ago, that we have the earliest evidence of vertebrate
26 scavenging where a temnospondyl amphibian fed on the carcass of *Varanops*, a predatory

synapsid of the time (Reisz and Tsuji 2006). The absence of flying vertebrates in the Palaeozoic may have permitted terrestrial forms to take in a higher proportion of carrion in their diet.

Aquatic Scavengers

An aquatic environment presents challenges for direct observational studies and so, similar to the approaches involving extinct species, much work has approached the question of scavenging propensity from an energetics perspective. Although as with the aerial and terrestrial environments we have evidence of facultative scavenging among aquatic species. For example, the remains of a mosasaur and a terrestrial hadrosaur were discovered with embedded teeth from a Cretaceous shark *Squalicorax* (Schwimmer et al. 1997). As well as a likely instance of scavenging between a 4-million-year-old white shark (*Carcharodon*) and mysticete whale from Peru (Ehret et al. 2009). The existence of an obligate scavenger in a marine setting is uncertain (Britton and Morton 1994, Smith and Baco 2003, Ruxton and Houston 2004a, Ruxton and Bailey 2005). Depending on the species a carcass in this environment either floats or descends to the sea floor. In this latter low-light environment detection distances are far lower (< 100 m) than they would be in the air. As such, animals detect resources through chemo- and mechanoreception more so than through vision (Ruxton and Houston 2004a). However, water is a medium that is conducive to low-cost movement (Tucker 1975) and so may be able to support an obligate scavenging fish (Ruxton and Houston 2004a, Ruxton and Bailey 2005). Benbow et al. (2015) do note that "some benthic scavengers (e.g., hagfish: family Myxinidae) rely on necrophagy for a large portion of their diet and may indeed be obligate scavengers".

Extant aquatic snakes are deemed as having the most suitable physiology and environment for scavenging. A hypothesis put forth by Sazima and Strüssmann (1990)

1 argued that chemical gradients in water would allow for a relatively easier detection of
2 carrion. This gained some support from DeVault and Krochmal (2002), who found a
3 preponderance of aquatic snake species in their review of this behaviour.

4 The presence of occasional bounties of carrion in the form of whale falls has led some
5 researchers to investigate if a scavenger could survive by seeking out these remains
6 exclusively. Ruxton and Bailey (2005) argued that although this is energetically feasible it's
7 ecologically unlikely. Any animal that could seek out such whale carcasses is unlikely to have
8 ignored other types of carrion. Although no aquatic species have ever exceeded the size of
9 whales, some enormous animals have evolved in this environment before the evolution of
10 whales, including *Leedsichthys*, a bony fish from the Jurassic Period, that weighed in excess
11 of 20 tonnes. Thus, the energetic feasibility of a marine scavenger has a long history. One
12 point of interest is that of the whaling industry, which provided a bonanza of floating
13 carcasses especially during the 20th century (Whitehead and Reeves 2005). This meant Killer
14 Whales *Orcinus orca* could switch from hunting to scavenging, a switch made that much
15 easier by the noise of the whaling vessels that would effectively ring the "dinner-bells"
16 (Whitehead and Reeves 2005). Early whales such as *Basilosaurus* seem to fit into the same
17 niche as Killer Whales and we have some evidence for scavenging in this group as well
18 (Fahlke 2012).

19 Ecological Role

20 It is recognised that scavengers keep energy flows at a higher trophic level in food webs than
21 decomposers because they consume relatively more carrion (DeVault et al. 2003). They are
22 also hugely important for the dispersal of nutrients (Benbow et al. 2015). Consider the
23 diversity of animals that can end up feeding at the carcass of an elephant. Here we have an
24 incredibly dense and nutrient rich patch that ends up being distributed widely. In the absence

1 of vertebrate scavengers, invertebrates and microorganisms would consume the carcass in-situ
2 or at least distribute the constituent nutrients over a much shorter range. This effect has
3 been magnified as vertebrates evolved certain key traits that allowed them to range farther,
4 namely an upright gait, an endothermic metabolism and of course, flight. To quantify this
5 effect with a simple example we can turn to some allometric relationships relating sustainable
6 travelling speed to body mass. In the case of mammals and reptiles these are $1.15 * \text{body mass (kg)}^{0.12}$
7 and $0.23 * \text{body mass (kg)}^{0.12}$ respectively (Ruxton and Houston 2004b). We
8 can insert these into a foraging radius model $((\text{duration} * \text{speed})/2)/1000$ for a 12 hour
9 foraging day which shows that while a 10 kg reptile can range 6.5 km an equally sized
10 mammal can range nearly 33 km (Enstipp et al. 2006). Thus, in an ecological context, the
11 evolution of these steps coupled with the ability to scavenge resulted in a world with a far
12 more widely distributed nutrient landscape.

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