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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 then overcome the
4 agents of decay produced by the action of microorganisms on the carcass (Ruxton et al.
5 2014). The idea of scrounging from predator kills is undermined by studies showing that in
6 the majority of ecosystems more animals die from disease and starvation than predation
7 (Benbow et al. 2015). Thus, any animal existing as a scavenger must maximise its detection
8 capabilities and minimise its locomotory costs (Ruxton and Houston 2004b). The habitat
9 must also be productive enough to sustain an animal biomass that will eventually produce
10 carcasses.

11 **Aerial Scavengers**

12 Vultures represent the best known scavengers on Earth. These birds consist of two
13 convergent groups, from the old and the new world and represent the only example of
14 obligate vertebrate scavengers today. Given their unique position, they have been extensively
15 studied to determine what adaptations they possess that allows them to so flourish in this
16 niche. Underscoring their prowess are studies such as Ogada et al. (2012) who note a three
17 fold increase in carcass persistence times in the absence of vultures. As such, we can begin by
18 exploring the adaptations and the environments of vultures to draw comparisons with other
19 scavenging species and *their* environments.

20 Species capable of flight have effectively added an extra spatial dimension, i.e. the
21 vertical component, to their sensory environment over land animals. This allows them to look
22 down on a landscape where they are unencumbered by obstacles that would obstruct the view
23 of a terrestrial scavenger. Such an ability has obvious benefits in detecting carrion. Vultures
24 are known to have impressive visual acuity with one estimate indicating Lappet-faced

1 Vultures (*Torgos tracheliotus*) are capable of detecting a 2 metre carcass over 10 km away
2 (Spiegel et al. 2013). We know that many birds exist as facultative scavengers; storks, eagles,
3 corvids, are all known to take substantial quantities of carrion in their diet. And eagles in
4 particular are known to have highly developed visual abilities. It follows from this that the
5 evolution of flight allowed aerial animals to detect far more carrion than their terrestrial
6 counterparts (Lisney et al. 2013).

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

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

19 Flight is also a cheaper means of locomotion than running (Tucker 1975). This advantage
20 can be extended further in larger species by engaging in soaring instead of flapping flight,
21 which is even cheaper still (approximately twice BMR) (Hedenstrom 1993). The benefits this
22 confers are clear from the information we have on the enormous foraging ranges of some
23 seabirds and accipiters (Bamford et al. 2007). Clearly, it would be pointless to have incredible
24 detection abilities and not have a cost efficient movement to benefit from it. Although, as
25 with detection ability, the environment has a role to play here. Vultures and eagles tend to
26 soar using thermals and if these air pockets don't form, say on a cloudy day, the bird is

grounded (Mundy et al. 1992). In many habitats (e.g. the arctic) it is simply not possible for sufficiently powerful thermals to form and as a consequence large-bodied vultures cannot exist. The upshot of this is that terrestrial carnivores like bears and wolves take more carrion (DeVault et al. 2003).

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

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

The only other vertebrate group capable of powered flight are the bats where scavenging has not been recorded to our knowledge. Their visual acuity is famously poor and

1 echolocation does not lend itself to discovering immobile carrion. Their small size and poor
2 terrestrial ability would also count against them at a carcass. The bat fossil record is
3 notoriously poor owing to their fragile skeletons so we are unable to determine if extinct
4 species were more suited to this lifestyle.

5 **Terrestrial Scavengers**

6 A simplification of terrestrial, vertebrate scavengers is one of them existing in a
7 two-dimensional plane while foraging for carrion directly. They can detect carcasses at a
8 range that is defined by the radius of their sensory organs, usually the visual and olfactory
9 senses. As a consequence, they have a much more restricted view of the landscape than do
10 aerial foragers. No contemporary terrestrial vertebrate exists as an obligate scavenger but
11 most if not all are facultative scavengers to some extent. Ruxton and Houston (2004b) offer
12 a reason for this in that the traits that allow for vultures to exist as scavengers undermined
13 their ability to hunt but that the same forces have not prevented mammals from doing so.
14 The same authors calculated that "a 1 tonne mammal or reptile, in an ecosystem yielding
15 carrion at densities similar to the current Serengeti, could have met its energy requirements if
16 it could detect carrion over a distance of the order of 400–500 m." (Ruxton and Houston
17 2004b).

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

23 Similar to vultures they have well developed sensory organs, particularly in olfaction
24 whereby they can detect a rotting carcass 2 km downwind. They have a characteristic

1 "rocking horse gait" which allows them to cover great distances efficiently. A major difficulty
2 for terrestrial scavengers is competition with vultures. Nocturnal behaviour in the Hyaenidae in
3 general has been put forth as an adaptation to reduce competition with these exclusively
4 diurnal birds (Gittleman 2013). The bone crushing ability of hyenas reveals another useful
5 scavenger trait. Since carrion is not dispatched directly, often the most easily accessible and
6 choicest components of the carcass will be missing or, if present, will be fought over. Being
7 able to extract nutrients from remnants gives the scavenger a great advantage. Osteophagy
8 is known across a range of terrestrial carnivores. Some fat-rich mammalian bones have an
9 energy density (6.7 kJ/g) comparable with that of muscle tissue, making skeletal remains an
10 enticing resource (Brown 1989). This ability reached its zenith among hyenas with the
11 evolution of the 110 kg *Pachycrocuta brevirostris* during the Pliocene (Palmqvist et al.
12 2011). Some work on extinct sabretooths suggests they may have left a large amount of food
13 for would-be scavengers because of their unique skull morphology. As a result the decline of
14 Machairodontinae sabretooths has been offered as an explanation for the extinction of *P*
15 *brevirostris* (Palmqvist et al. 2011).

16 The order Carnivora sees its origins in the Eocene where it split into the Caniforma and
17 Feliforma. And many of the aforesaid adaptations for scavenging are found in these other
18 major terrestrial mammalian carnivores. Though the specific mix of features realised in
19 hyenas suggest this is the model organism for terrestrial scavenging among mammals in the
20 past. For example, the bone-crushing dogs that evolved during the Oligocene (subfamily
21 Borophaginae) have been compared to hyenas in terms of their feeding ecology
22 (Van Valkenburgh et al. 2003, Martín-Serra et al. 2016). Certainly, it is profitable to compare
23 extant terrestrial species to their prehistoric forebears given the dominance of mammalian
24 carnivores since the Eocene.

25 Interestingly such comparisons have given insight into the feeding ecology of early
26 hominins who, for instance, had the ability to craft tools for breaking open bones (Hone and

1 Rauhut 2010, Blasco et al. 2014). The question of where our ancestors placed on the
2 hunter-scavenger axis during the Plio-Pleistocene has been a matter of debate for years. A
3 recent study investigating potential scavenging opportunities for hominins in Kenya found
4 that, even when discounting bone material, there is a substantial amount of scavengeable
5 meat left on predated remains; sufficient to sustain the requirements of an adult male *Homo*
6 *erectus* (Pobiner 2015). In some historical hominin-inhabited areas there were a greater
7 number of felids than hyenids. This is significant because hyenas will leave far less flesh on a
8 carcass than a felid such as a sabretooth enabling contemporaneous hominins to benefit
9 (Pobiner 2015). The intelligence, resultant tool-use and cooperative nature of hominins
10 meant they could likely adapt to take on more or less carrion depending on their
11 environment.

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

1 Unsurprisingly, given their enduring appeal, the prevalence of scavenging has been
2 explored in the carnivorous, theropod dinosaurs. These animals ranged from the chicken-sized
3 to the whale-sized all of which were bipedal. They are quite alien to anything we know today
4 which restricts our ability to understand their ecology far more so than extinct mammals
5 (Weishampel et al. 2004). Of relevance, are the questions that still persist about their
6 metabolism (Grady et al. 2014) and sensory perception. We do know that they walked with
7 the erect gait of mammals or birds rather than the sprawling gait of lizards and that they
8 were most likely facultative scavengers (DePalma et al. 2013). Much work has focused on the
9 existence of the behaviour in *Tyrannosaurus rex* (Ruxton and Houston 2003, Carbone et al.
10 2011) but a recent energetics study investigated the likely prevalence of scavenging across a
11 range of body sizes. In it the authors demonstrated that species of intermediate body masses
12 (approx. 500 kg) would have gained the most benefit from scavenging. This was the result of
13 gut capacity limitations and the effects of competition at the carcass. At the larger extreme
14 this owes to the fact that gut capacity doesn't scale isometrically with body mass so the
15 benefits of greater mass level off; there's only so much food an individual can consume at a
16 single sitting (Calder 1996). For the smaller species, larger competitors would have prevented
17 their access to carrion.

18 As we discussed for the case of Cenozoic carnivores, osteophagy could be extremely
19 beneficial to a scavenger. In Mesozoic systems some extremely large theropod dinosaurs had
20 a morphology which suggests an ability to process bone e.g. the robust skull and dentition of
21 *T. rex*. There is direct evidence that *T. rex* did this in the form of distinctive wear marks on
22 its tooth apices (Farlow and Brinkman 1994, Schubert and Ungar 2005) and the presence of
23 bone fragments in its coprolites (Chin et al. 1998). The animal also had an enormous bite
24 force, with one estimate putting it at 57000 Newtons (Bates and Falkingham 2012). This is
25 noted as being powerful enough to break open skeletal material (Rayfield et al. 2001).
26 Osteophagy may have been even more viable during this era because the body mass

1 distribution of herbivores tended to be skewed towards larger sizes (O'Gorman and Hone
2 2012). When we couple this with the fact that skeletal mass scales greater than linearly with
3 body mass (Prange et al. 1979) there would have been a lot of bone material to consume in
4 the environment provided an animal had the biology to process it (Chure and Fiorillo 1997).

5 Of course, tetrapod terrestrial dominance predates the evolution of the dinosaurs. It is in
6 the Permian, almost 300 millions years ago, that we have the earliest evidence of vertebrate
7 scavenging where a temnospondyl amphibian fed on the carcass of *Varanops*, a predatory
8 synapsid of the time (Reisz and Tsuji 2006). The absence of flying vertebrates in the
9 Palaeozoic may have permitted terrestrial forms to take in a higher proportion of carrion in
10 their diet. As noted earlier, a system similar to the Serengeti in productivity could have
11 supported a terrestrial scavenger (Ruxton and Houston 2004b).

12 **Aquatic Scavengers**

13 An aquatic environment presents challenges for direct observational studies and so, similar to
14 the approaches involving extinct species, much work has approached the question of
15 scavenging propensity from an energetics perspective. Although as with the aerial and
16 terrestrial environments we have evidence of facultative scavenging among aquatic species.
17 For example, the remains of a mosasaur and a terrestrial hadrosaur were discovered with
18 embedded teeth from a Cretaceous shark *Squalicorax* (Schwimmer et al. 1997). As well as a
19 likely instance of scavenging between a 4-million-year-old white shark (*Carcharodon*) and
20 mysticete whale from Peru (Ehret et al. 2009). The existence of an obligate scavenger in a
21 marine setting is uncertain (Britton and Morton 1994, Smith and Baco 2003, Ruxton and
22 Houston 2004a, Ruxton and Bailey 2005). Depending on the species a carcass in this
23 environment either floats or descends to the sea floor. In the latter low-light environment,
24 detection distances are far lower (< 100 m) than they would be in the air. As such, animals

1 detect resources through chemo- and mechanoreception more so than through vision (Ruxton
2 and Houston 2004a). However, water is a medium that is conducive to low-cost movement
3 (Tucker 1975) and so may be able to support an obligate scavenging fish (Ruxton and
4 Houston 2004a, Ruxton and Bailey 2005). Benbow et al. (2015) do note that "some benthic
5 scavengers (e.g., hagfish: family Myxiniidae) rely on necrophagy for a large portion of their
6 diet and may indeed be obligate scavengers".

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

12 The presence of occasional bounties of carrion in the form of whale falls has led some
13 researchers to investigate if a scavenger could survive by seeking out these remains
14 exclusively. Ruxton and Bailey (2005) argued that although this is energetically feasible it's
15 ecologically unlikely. Any animal that could seek out such whale carcasses is unlikely to have
16 ignored other types of carrion. Although no aquatic species have ever exceeded the size of
17 whales, some enormous animals have evolved in this environment before the evolution of
18 whales, including *Leedsichthys*, a bony fish from the Middle Jurassic (174.1-163.5 Mya), that
19 weighed in excess of 20 tonnes. Thus, the energetic feasibility of a marine scavenger has a
20 long history. One point of interest is that of the whaling industry, which provided a bonanza
21 of floating carcasses especially during the 20th century (Whitehead and Reeves 2005). This
22 meant Killer Whales *Orcinus orca* could switch from hunting to scavenging, a switch made
23 that much easier by the noise of the whaling vessels that would effectively ring the
24 "dinner-bells" (Whitehead and Reeves 2005). Early whales such as *Basilosaurus* seem to fit
25 into the same niche as Killer Whales and we have some evidence for scavenging in this group
26 as well (Fahlke 2012).

1 **Ecological Role**

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

19 **The Role of Climate**

20 The geological record shows the Earth has undergone radical fluctuations in temperature.
21 This will have had a significant bearing on the availability of carrion. A 10°C increase in
22 ambient temperature can double carcass decomposition rates (Benbow et al. 2015). Oceanic
23 productivity, decomposition rates and habitat structure are all impacted by climactic
24 conditions. Benbow et al. (2015) points to a series of studies showing how microbes and

1 invertebrates benefit at higher temperatures to the detriment of vertebrate scavengers "above
2 20°C vertebrates were able to detect and consume only 19% of small-mammal carcasses,
3 whereas at temperatures below 18°C, vertebrates consumed 49% of carcasses". Furthermore,
4 "carcass decomposition occurs more rapidly in warm, moist habitats when compared with
5 more xeric habitats."

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