

1 **Running title:** Scavenging in vertebrates

2 **Number of words:** ~9999

3 **Date of submission:** March 22, 2016

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

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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

Introduction

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

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. Thus, any animal existing as a scavenger must
4 minimise its locomotory costs and maximise its detection capabilities (Ruxton and Houston
5 2004b). Once found, the scavenger has to process the carrion and overcome the agents of
6 decay produced by the action of microorganisms on the carcass (Ruxton et al. 2014). The
7 habitat must also be productive enough to sustain an animal biomass that will eventually
8 produce carcasses. We can draw on the image of a scavenger moving through its
9 environment, searching for food and trying to process it efficiently as we explore the
10 prevalence of this behaviour through time.

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. The families from which modern vultures arose, the
15 Accipitridae and Cathartidae, appear during the Palaeocene (66 - 56 Mya) (Jetz et al. 2012,
16 Jarvis et al. 2014). Given their unique position, they have been extensively studied to
17 determine what adaptations they possess that allows them to so flourish in this niche.
18 Underscoring their prowess are studies such as Ogada et al. (2012) who note a three fold
19 increase in carcass persistence times in the absence of vultures. As such, we can begin by
20 exploring the adaptations and the environments of vultures to draw comparisons with other
21 scavenging species and *their* environments.

1 **Locomotion**

2 Flight is a cheaper means of locomotion than running (Tucker 1975). This advantage can be
3 extended further in larger species by engaging in soaring instead of flapping flight, which is
4 even cheaper still (approximately twice BMR) (Hedenstrom 1993). The benefits this confers
5 are clear from the information we have on the enormous foraging ranges of many vultures
6 (Spiegel et al. 2013). Avian flight originates in the Late Jurassic (163.5-145 Million years ago
7 - Mya), coincident with the fossils of *Archaeopteryx lithographica* so many of these benefits
8 would have been realised from that point on for carnivorous birds. However, vertebrate flight
9 is much older than this where pterosaurs predate bird origins by a considerable margin in the
10 Late Triassic (235-201.3 Mya). Scavenging in this diverse group has been hypothesised many
11 times before. Certain clades of these animals could reach enormous sizes (e.g. Azhdarchids
12 with wingspans of 11 metres (Witton and Habib 2010)) and look to have engaged in soaring
13 flight (Witton and Habib 2010).

14 The only other vertebrate group capable of powered flight are the bats where scavenging
15 has not been recorded to our knowledge.

16 **Detection**

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

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

Moreover, having a panoramic view means being able to gather a wealth of information from other foragers, be they conspecifics or other species (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).

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

Clearly, it would be pointless to have incredible ranging abilities and not have the sensory architecture to benefit from it.

Processing

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.

Large body size confers substantial dominance and starvation-resistance benefits (Ruxton

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

7 Although Witton and Naish (2008) argued that neck inflexibility and straight, rather than
8 hooked jaw morphology points against pterosaurs existing as *obligate* scavengers, Azhdarchid
9 terrestrial proficiency indicates they would have been comfortable foraging on the ground.
10 Indeed, extant Marabou Storks (*Leptoptilos crumenifer*) have a comparable morphology and
11 are noted facultative scavengers so it is reasonable to believe that certain pterosaurs behaved
12 similarly.

13 Returning to bats, their visual acuity is famously poor and echolocation would not lend
14 itself to discovering immobile carrion. Their small size and poor terrestrial ability would also
15 count against them at a carcass (Riskin et al. 2006). The bat fossil record is notoriously poor
16 owing to their fragile skeletons so we are unable to determine if extinct species were more
17 suited to this lifestyle (Eiting and Gunnell 2009). Big bats (which are better suited for
18 scavenging, following our previous argument) are typically frugivores and therefore probably
19 lack of adaptations for digesting the meat. Also carnivorous bats are mainly the microbats
20 which are insectivorous.

21 **Environment**

22 Vultures and eagles tend to soar using thermals and if these air pockets don't form, say on a
23 cloudy day, the bird is grounded (Mundy et al. 1992). In many habitats (e.g. the arctic) it is
24 simply not possible for sufficiently powerful thermals to form and as a consequence
25 large-bodied vultures cannot exist. The upshot of this is that terrestrial carnivores like bears

1 and wolves take more carrion (DeVault et al. 2003). The use of different sensory systems also
2 illustrates the impact of the environment. The relatively open savanna systems of Africa are
3 well suited to a visually dependent vulture whereas more forested areas would select for
4 species that have a well developed olfactory system (Houston 1986).

5 **Terrestrial Scavengers**

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

11 No contemporary terrestrial vertebrate exists as an obligate scavenger but most if not all
12 are facultative scavengers to some extent (Beasley et al. 2015). Ruxton and Houston (2004b)
13 offer a reason for this in that the traits that allow for vultures to exist as scavengers
14 undermined their ability to hunt but that the same forces have not prevented mammals from
15 doing so. Interestingly, the same authors calculated that “a 1 tonne mammal or reptile, in an
16 ecosystem yielding carrion at densities similar to the current Serengeti, could have met its
17 energy requirements if it could detect carrion over a distance of the order of 400–500
18 m.”(Ruxton and Houston 2004b).

19 **Locomotion**

20 As endotherms, mammals can sustain long bouts of energetically expensive activity. By
21 contrast, modern reptiles are ectothermic, limiting their activity periods. This is exacerbated
22 by the sprawling gait seen in many lizards which results in Carrier’s Constraint such that the
23 animal can’t move and breathe at the same time because the lateral movements impedes its

lungs (Carrier 1987). This manifests itself in aspects such as maximum sustainable speed where an equivalent mammal has a six to seven fold increase (Ruben 1995). 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 $0.23 * \text{body mass (kg)}^{0.12}$. 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). Hyenas extend this advantage with their characteristic "rocking horse gait" which allows them to cover great distances efficiently (Jones et al. 2015).

Unsurprisingly, given their enduring appeal, the prevalence of scavenging has been explored in the carnivorous, theropod dinosaurs. These animals ranged from the chicken-sized to the whale-sized all of which were bipedal. They are quite alien to anything we know today which restricts our ability to understand their ecology far more so than extinct mammals (Weishampel et al. 2004). Of relevance, are the questions that still persist about their metabolism (Grady et al. 2014). We do know that they walked with the erect gait of mammals or birds rather than the sprawling gait of lizards and that they were most likely facultative scavengers (Weishampel et al. 2004, DePalma et al. 2013).

Of course, tetrapod terrestrial dominance predates the evolution of the dinosaurs. It is in the Permian, almost 300 millions years ago, that we have the earliest evidence of vertebrate scavenging where a temnospondyl amphibian fed on the carcass of *Varanops*, a predatory synapsid of the time (Reisz and Tsuji 2006).

Detection

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, usually the visual and olfactory

senses. As a consequence, they have a much more restricted view of the landscape than do aerial foragers. Similar to vultures hyenas have well developed sensory organs, whereby they can smell a rotting carcass 4 km away and can hear the vocalisations of conspecifics at a distance of 10 km (Mills 1989). Using the same approach Spiegel et al. (2013) used to determine the visual acuity of vultures we found a Spotted hyena could resolve a 2 metre target at 1 km distance.

Processing

The bone crushing ability of hyenas reveals another useful scavenger trait. Since carrion is not dispatched directly, often the most easily accessible and choicest components of the carcass will be missing or, if present, will be fought over. Being able to extract nutrients from remnants gives the scavenger a great advantage. Osteophagy is known across a range of terrestrial carnivores and given some fat-rich mammalian bones have an energy density (6.7 kJ/g) comparable with that of muscle tissue, it makes skeletal remains an enticing resource (Brown 1989). This ability reached its zenith among hyenas with the evolution of the 110 kg *Pachycrocuta brevirostris* during the Pliocene (Palmqvist et al. 2011). Some work on extinct sabretooths suggests they may have left a large amount of food for would-be scavengers because of their unique skull morphology. As a result, the decline of Machairodontinae sabretooths has been offered as an explanation for the extinction of *P brevirostris* (Palmqvist et al. 2011). The order Carnivora sees its origins in the Middle Eocene (56-33.9 Mya) where it split into the Caniforma and Feliforma. And many of the aforesaid adaptations for scavenging are found in these other major terrestrial mammalian carnivores. Though the specific mix of features realised in hyenas suggest this is the model organism for terrestrial scavenging among mammals in the past. For example, the bone-crushing dogs that evolved during the Oligocene (subfamily Borophaginae) have been compared to hyenas in terms of their feeding ecology (Van Valkenburgh et al. 2003, Martín-Serra et al. 2016). Certainly, it is

1 profitable to compare extant terrestrial species to their prehistoric forebears given the
2 dominance of mammalian carnivores since the Eocene.

3 Interestingly such comparisons have given insight into the feeding ecology of early
4 hominins who, for instance, had the ability to craft tools for breaking open bones (Blasco
5 et al. 2014). The question of where our ancestors placed on the hunter-scavenger axis during
6 the Plio-Pleistocene has been a matter of debate for years. A recent study investigating
7 potential scavenging opportunities for hominins in Kenya found that, even when discounting
8 bone material, there is a substantial amount of scavengeable meat left on predated remains;
9 sufficient to sustain the requirements of an adult male *Homo erectus* (Pobiner 2015). In
10 some historical hominin-inhabited areas there were a greater number of felids than hyenids.
11 This is significant because hyenas are likely to have left far less flesh on a carcass than a felid
12 such as a sabretooth enabling contemporaneous hominins to benefit (Pobiner 2015).

13 The intelligence, resultant tool-use and cooperative nature of hominins meant they could
14 likely adapt to take on more or less carrion depending on their environment (Moleón et al.
15 2014).

16 When it comes to reptiles they possess an advantage here, in that over the course of a
17 year their food requirements can be 30 times smaller than an endotherm of equal size (Nagy
18 2005). Any adaptations that reduce energetic costs are likely to be selected in scavengers.
19 DeVault and Krochmal (2002) suggest this is an avenue for scavenging in snakes because
20 they “exhibit exceedingly low maintenance metabolisms, and most can survive on a few scant
21 feedings per year. It is, therefore, possible for snakes to rely largely on infrequent, less
22 energy-rich meals.” In the same review the authors found occurrences of scavenging spread
23 across five families of snakes and stated that this behaviour is “far more common than
24 currently acknowledged.”(DeVault and Krochmal 2002). The same reasoning can be applied
25 to crocodiles and their allies (Forrest 2003).

26 Much work has focused on the existence of scavenging in dinosaurs by using simple

energetics approaches that typically focused on a single species namely *Tyrannosaurus rex* (Ruxton and Houston 2003, Carbone et al. 2011) but a recent modelling study investigated the likely prevalence of scavenging across a range of body sizes. In it the authors demonstrated that species of intermediate body masses (approximately 500 kg) would have gained the most benefit from scavenging. This was the result of gut capacity limitations and the effects of competition at the carcass. At the larger extreme this owes to the fact that gut capacity doesn't scale isometrically with body mass so the benefits of greater mass level off; there's only so much food an individual can consume at a single sitting (Calder 1996). For the smaller species, larger competitors would have prevented their access to carrion.

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

Environment

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 exclusively diurnal birds (Gittleman 2013).

Osteophagy may have been even more viable during the Mesozoic era because the body mass distribution of herbivores tended to be skewed 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

1 consume in the environment provided an animal had the biology to process it (Chure and
2 Fiorillo 1997). As we discussed earlier, osteophagy could be extremely beneficial to a
3 scavenger.

4 The absence of flying vertebrates in the Palaeozoic may have permitted terrestrial forms
5 to take in a higher proportion of carrion in their diet. As noted earlier, a system similar to the
6 Serengeti in productivity could have supported a terrestrial scavenger (Ruxton and Houston
7 2004b). Indeed, in systems that were dominated by large ectothermic or mesothermic
8 vertebrates the same primary productivity would have supported a greater biomass (McNab
9 2009). The upshot of this is there was a higher biomass of herbivores dying and offering
10 scavenging opportunities. Predators were large bodied too compared to extant mammalian
11 predators (McNab 2009), and so, especially if they were ectothermic, could last longer
12 between meals rendering scavenging a more attractive behaviour relative to predation.

13 Scavenging behaviour might have evolved as soon as the first terrestrial tetrapods
14 evolved. In fact, some of the earlier tetrapods tracks dating back to the early Middle
15 Devonian (393.3 - 387.7 Mya) were found in intertidal environments (Niedzwiedzki et al.
16 2010). These environments are isolated from marine systems twice a day leaving potential
17 carrion unexploited by marine vertebrates. Niedzwiedzki et al. (2010) suggests that these
18 environments "would thus have allowed marine ancestors of tetrapods gradually to acquire
19 terrestrial competence while accessing a new and essentially untouched resource."

20 **Aquatic Scavengers**

21 Primary productivity is lower in almost all aquatic systems than terrestrial systems (except
22 deserts) so as we go up the food chain the density of carcasses worth scavenging is going to
23 be lower. But it is certainly known to occur in many aquatic vertebrates. An aquatic
24 environment presents challenges for direct observational studies and so, similar to the

1 approaches involving extinct species, much work has approached the question of scavenging
2 propensity from an energetics perspective. Although, as with the aerial and terrestrial
3 environments we have evidence of facultative scavenging among aquatic species. For
4 example, the remains of a mosasaur and a terrestrial hadrosaur were discovered with
5 embedded teeth from a Cretaceous shark, *Squalicorax* (Schwimmer et al. 1997). As well as a
6 likely instance of scavenging between a 4-million-year-old white shark (*Carcharodon*) and
7 mysticete whale from Peru (Ehret et al. 2009).

8 The existence of an obligate scavenger in a marine setting is uncertain (Britton and
9 Morton 1994, Smith and Baco 2003, Ruxton and Houston 2004a, Ruxton and Bailey 2005).
10 Depending on the species, a carcass in this environment either floats or descends to the sea
11 floor (Whitehead and Reeves 2005). In the latter low-light environment, visual detection
12 distances are far lower (< 100 m) than they would be in the air. As such, animals detect
13 resources through chemo- and mechanoreception more so than through vision (Ruxton and
14 Houston 2004a). However, water is a medium that is conducive to low-cost movement
15 (Tucker 1975) and so may be able to support an obligate scavenging fish (Ruxton and
16 Houston 2004a, Ruxton and Bailey 2005). Beasley et al. (2015) do note that "some benthic
17 scavengers (e.g., hagfish: family Myxiniidae) rely on necrophagy for a large portion of their
18 diet and may indeed be obligate scavengers".

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

24 The presence of occasional bounties of carrion in the form of whale falls has led some
25 researchers to investigate if a scavenger could survive by seeking out these remains
26 exclusively. Ruxton and Bailey (2005) argued that although this is energetically feasible it's

1 ecologically unlikely. Any animal that could seek out such whale carcasses is unlikely to have
2 ignored other types of carrion. Although no aquatic species have ever exceeded the size of
3 whales, some enormous animals have evolved in this environment before the evolution of
4 whales, including *Leedsichthys*, a bony fish from the Middle Jurassic (174.1-163.5 Mya), that
5 weighed in excess of 20 tonnes. Thus, the energetic feasibility of a marine scavenger has a
6 long history. One point of interest is that of the whaling industry, which provided a bonanza
7 of floating carcasses especially during the 20th century (Whitehead and Reeves 2005). This
8 meant Killer Whales (*Orcinus orca*) could switch from hunting to scavenging, a switch made
9 that much easier by the noise of the whaling vessels that would effectively ring the
10 "dinner-bells" (Whitehead and Reeves 2005). Early whales such as *Basilosaurus* seem to fit
11 into the same niche as Killer Whales and we have some evidence for scavenging in this group
12 as well (Fahlke 2012). A final point to make is that vertebrates are relatively rarer in aquatic
13 environments, because even large animals can get support from the buoyancy of the water
14 without needing a backbone.

15 They are also hugely important for the dispersal of nutrients (Beasley et al. 2015).
16 Consider the diversity of animals that can end up feeding at the carcass of an elephant. Here
17 we have an incredibly dense and nutrient rich patch that ends up being distributed widely. In
18 the absence of vertebrate scavengers, invertebrates and microorganisms would consume the
19 carcass in-situ or at least distribute the constituent nutrients over a much shorter range. This
20 effect has been magnified as vertebrates evolved certain key traits that allowed them to range
21 farther, namely an upright gait, an endothermic metabolism and of course, flight. To quantify
22 this effect with a simple example we can turn to some allometric relationships relating
23 sustainable travelling speed to body mass. In the case of mammals and reptiles these are
24 $1.15 * \text{body mass (kg)}^{0.12}$ and $0.23 * \text{body mass (kg)}^{0.12}$ We can insert these into a
25 foraging radius model $((\text{duration} * \text{speed})/2)/1000$ for a 12 hour foraging day which shows
26 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 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 terms of specific habitats, it has been shown that decomposition is greater in warm and moist areas versus more xeric ones (Beasley et al. 2015). Moreover, oceanic productivity and habitat structure are all impacted by climactic conditions. The impacts these can have on scavengers have been empirically supported e.g. Beasley et al. (2015) who point to a series of studies showing how microbes and invertebrates benefit at higher temperatures to the detriment of vertebrate scavengers such that “above 20°C vertebrates were able to detect and consume only 19% of small-mammal carcasses, whereas at temperatures below 18°C, vertebrates consumed 49% of carcasses”.

Acknowledgments

A lot of people are to thank here.

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