

July 13, 2016

Company name  
Street  
City  
Country

To the editor

We would like to thank the editor, subject editor and reviewers for their comments. By bringing attention to elements of the manuscript that require more careful communication we believe that you have helped us to significantly improve our manuscript. In this submission we have clarified these areas and added a body of work to bolster the conclusions drawn from our work. Please see below where we consider each of your points in turn.

Reviewer: 1

Comments to the Author This paper attempts to synthesize literature on traits that enable scavenging behavior in extant and extinct vertebrates. The paper is mostly well written, and most (but not all) pertinent literature sources are included. I do worry about the lack of novelty of the manuscript, and what I perceived as haphazard organization. Here are some specific issues that should be addressed in my opinion:

1. Abstract: Scavenging can be difficult to observe, but probably no more so than predation. Also, using experimental carcasses, scavenging is actually quite easy to observe.
2. Abstract: You should point out that your scale of scavenging is only qualitative; you made no attempt to quantify such traits.
3. Introduction: Much of this section seems to follow DeVaults (2003) review paper on scavenging. In fact, there is almost nothing new here that is not covered in that earlier review.
4. Introduction: You mention that you will use other methods in order to discern the most suitable morphologies but you don't say what they are. What other methods are you talking about?
5. I think that early on in the paper you need to define obligate and facultative scavengers and then throughout the paper, specify which you are referring to. For example, in the first sentence of the Detection section, you talk about known scavengers, but it is unclear if you really mean obligate scavengers. Nearly all carnivorous vertebrates are scavengers at least to some extent, so you need to elaborate on what you mean when you talk about scavengers.
6. Last sentence of Introduction: Again, you propose a scale of scavenging, but

without quantification, it is unclear how useful this scale is.

7. Page 6, 12: In your discussion of aquatic scavengers, you might want to refer to Beasley et al. (2012; *Oikos* 121:1021-1026).

8. Page 6: Why is jaw morphology likely to define scavengers? Please elaborate.

9. Page 9: It is true that carrion can comprise a large percentage of a hyenas diet, but your text seems misleading. Most studies have shown that most of a hyenas diet is from predation. For example, see Cooper et al. (1999; *Afr. J. Ecol.* 37:149160) and Gasaway et al. (1991; *Afr. J. Ecol.* 29: 6475).

10. Your section on Handling Time is so short that I think it should be cut or combined with another section.

Reviewer: 2

Comments to the Author This article is a review of the literature what the authors term a "natural history" of scavenging. They have approached the topic from the perspective of ecological variables (and other variables that condition them) in optimal foraging theory including encounter rate and handling time, but also metabolism, locomotion (e.g soaring and swimming), detection, prey availability, competition, and food processing. They describe many useful examples of the behavior and ecology of obligate and facultative scavengers. But I think they often go to far in their assumptions in trying to weave these examples together in a synthetic way. Some examples are inferring scrounging behaviors in flying pterosaurs (page 11), assuming that hominins used vultures to identify scavenging opportunities (page 11), surmising that scavenging evolved with the earliest tetrapods based on "potential carrion unexploited by marine vertebrates" (page 12). There is a lot of "these researchers have suggested X" and then taking that as a given fact.

While the authors distinguish between obligate and facultative scavenging, they tend to lump them together when it comes to constructing their arguments. In the end, is the argument about the former, or the latter? Is the real interest in whether species scavenge at all, what proportion of their resources are obtained by scavenging, or what the conditions are that produce facultative or obligate scavengers? They also seem to ignore flexibility in species' behaviors. For instance, while spotted hyenas are on their highly scavenging side of their Figures 1 and 2, in some ecosystems they hunt significant proportion of their prey. Similarly, lions can take a large proportion of their prey as scavenged, as the authors note. But to suggest, as they do in their abstract, that they can apply their scale of scavenging to any species at any time to judge how important scavenging was in its diet is frankly completely ignoring behavioral variability over time and space. It is substantially more difficult with fossil species for which we may know far fewer of the variables they list in Figure 1, in a nuanced way. Figure 2 does not display the diversity of scavengers through time, it displays examples of species that display observed or inferred scavenging behaviors. Diversity has

specific ecological definition(s) that are being ignored here.

If the authors chose to resubmit, I would suggest they organize their manuscript based on known information about modern species, known (e.g. bone processing by theropods) and inferred (e.g. scavenging in hominins) information about fossil species, and then try to draw broader conclusions. They might look to articles about other modern scavenging opportunities such as Capaldo and Peter's study of wildebeest drownings <http://www.sciencedirect.com/science/article/pii/S0305440385700398>, and suggestions that sabertooth cats which they claim were unable to feed on bones may have consumed more bone than penecontemporaneous dire wolves

In sum, while I think the aim of the article is a very worthwhile one, I think the authors cannot claim to have produced an all-encompassing model that can predict the presence or level of scavenging in any organism - because I think this simply cannot be done.

Finally, some of the perspectives of this manuscript overlap substantially with parts of Beasley et al. 2015 (pages 108-112), which is cited numerous times in the manuscript.

Reviewer: 3

Comments to the Author This is a well-written, enjoyable manuscript that assesses the functional traits associated to past and, mostly, current major vertebrate scavengers. As a result, the authors provide a sort of guide to identify the extent of scavenging behaviour among carnivores in both current and past ecosystems. I have several suggestions that should be considered before publication (please see below).

Major comments:

1. Invertebrates are ignored completely throughout the ms. Please specify in the Introduction that this review focuses on vertebrate scavengers. In this line, I recommend to include invertebrates at the end of the title to be more specific. Also, in the Competition section you mention competition with vertebrates and micro-organisms, but not with invertebrates. You should consider them in this section (and in Facilitation; see next point).
2. I found difficult to follow the main point of the paper because the ms is not well organized. Following a hierarchical order, I'd define four/five main sections: Introduction, The Challenges of Scavenging (this could be a subsection within the previous section), Encounter Rate (with four different subsections: Metabolism, Locomotion, Sensory Detection and Carcass Availability), Handling Time (which would include Food Processing) and Conclusion.

Moreover, Competition and Facilitation (I strongly encourage you to consider not only competitive, but also facilitative processes, which are mostly neglected in your review) should be treated as transversal factors that can modulate each

of the abovementioned parameters. Thus, I include them in a different section, or mention the competitive and facilitative processes related to each parameter within each subsection. Fig. 1 should be re-organized accordingly.

3. The use of the scientific literature on scavenging is deficient, especially for a review paper like this. A number of key references are missing, e.g., Selva & Fortuna (2007 *Proc. R. Soc. B* 274:1101-1108), Wilson & Wolkovich (2011 *TREE* 23:129-135), Beasley et al. (2012 *Oikos* 121:1021-1026), Corts-Avizanda et al. (2012 *Ecology* 93:2570-2579), Corts-Avizanda et al. (2014 *Ecology* 95:1799-1808), Molen et al. (2014 *Biol. Rev.* 89:1042-1054), Pereira et al. (2014 *Mammal Rev.* 44:44-55), Priquet et al. (2015 *Biol. Rev.* 90:1197-1214), Mateo-Toms et al. (2015 *Divers. Distrib.* 21:913-924), Molen & Snchez-Zapata (2015 *BioScience* 65:1003-1010), Moreno-Opo et al. (2016 *Behav. Ecol.*), Sebastin-Gonzlez et al. (2016 *Ecology* 97:95-105). Your literature synthesis might benefit from the reading of these articles, for instance regarding competitive and facilitative interactions among scavengers. Also, the review would be more informative and useful for readers. Next I mention some particular comments regarding the use of the references (I mention others in Minor comments):

Page 2, 1st sentence: but see Molen & Snchez-Zapata (2015); many of the most charismatic vertebrates of the world are scavengers. Rather than scavengers, what is not charismatic is probably scavenging.

We now refer to the behaviour rather than the species as lacking charisma.

Page 2, 13th line: Molen & Snchez-Zapata (2015) may be more appropriate than Koenig (2006) because the former is more general and not restricted to vultures. Page 2, lines 17th-18th: see Pereira et al. (2014) and Priquet et al. (2015) for reviews.

These references have been added.

Page 3, bottom paragraph, bottom line: this is not true, as scavenging may indirectly affect herbivore populations and thus carrion availability (see Molen et al. 2014 *Biol. Rev.*).

The potential for scavengers to affect carrion availability has been acknowledged.

Page 5, bottom paragraph, 1st sentence: Mateo-Toms et al. (2015) is more general than Kendall (2013). Page 8, 1st and 2nd sentences: see Pereira et al. (2014) and Priquet et al. (2015). Page 8, 3rd sentence: you may also cite DeVault et al. (2003) and Pereira et al. (2014).

These references have been added.

Page 8, 8th-17th lines: please reword; wild dogs hardly scavenge, while leopards and lions are frequent scavengers (see Pereira et al. 2014).

We have reworded this section to make the more general point that ambush

predators can rely more on hunting than can cursorial species, a point explicitly stated in the Pereira et al. (2014) article, which we now cite.

Page 11, 1st sentence: see Kane et al. (2014) and Molen et al. (2014 Biol. Rev.) for inter-specific interactions. Page 11, 4th sentence: Kane et al. (2014) is not appropriate here because it is about inter-specific interactions; use Corts-Avizanda et al. (2014) instead. Page 14, 2nd paragraph, 1st sentence: see also Molen et al. (2014 Biol. Rev.) and Pereira et al. (2014). Page 14, 2nd paragraph, 2nd sentence: see better Pereira et al. (2014) and Priquet et al. (2015). Page 14, bottom paragraph, 3rd sentence: you may also consider Moreno-Opo et al. (2016). Page 15, 2nd paragraph, 2nd sentence: see also Molen et al. (2014 Biol. Rev.) and Pereira et al. (2014).

All of these references have been added.

4. You should include more discussion about the importance of carcass size throughout the ms, as it has a strong influence on scavenging patterns and interactions among vertebrates and between vertebrates and smaller carrion consumers (e.g., see Molen et al. 2015).

Minor comments:

#### GENERAL

1. Please provide line numbers to facilitate the reviewing process.

Line numbers have now been included.

#### ABSTRACT

2. You could remove , the first to our knowledge.

This has been removed.

3. Also, you could mention some relevant specific findings of your synthesis.

#### THE CHALLENGES OF SCAVENGING

4. Page 3, 1st sentence: often difficult to predict compared to what? Please specify. There are many examples in which carrion is highly predictable, e.g., during salmon spawning (see also Pereira et al. 2014).

#### ENCOUNTER RATE

5. Page 3, bottom paragraph, 3rd line: change Alternatively to Also?

This has been changed.

#### METABOLISM

6. Page 4, 1st sentence: the sporadic nature of carrion; please explain.

#### LOCOMOTION

7. Page 4, bottom paragraph, 1st sentence: change inherent to relative.

This has been changed.

8. Page 4, bottom paragraph, 3rd sentence: remove , paradoxically,.

This has been deleted.

9. Page 5, 2nd paragraph, 1st sentence: change appear to appeared. Also, specify Mya for the Cretaceous period.

This has been changed.

10. Page 9, top paragraph: please be more cautious in your assertion, as cooperation skills and tools of early hominins probably allowed them to defend and usurp carcasses from more powerful scavengers.

We have changed this paragraph and take into account the authors' reference to tool use and sociality in hominins. The point is that even with these advantages, running to a carcass over long distances still wasn't energetically sensible.

#### DETECTION

11. Page 11, top and 2nd paragraph, 1st sentence: this is about facilitation. As said above, facilitative processes may affect other parameters as well, not only the ability to detect carrion.

12. Page 11, last sentence: explain why wind speed affects the olfactory capacity of an aquatic species.

#### PREY AVAILABILITY

13. Id change this title to Carcass Availability, which is more specific.

This has been changed.

14. Among the different components of carcass availability, e.g., abundance, duration, predictability and accessibility, in this section you only talk about abundance and duration. You should also discuss about carcass predictability (e.g., see Corts-Avizanda et al. 2012) and carcass accessibility (e.g., see DeVault & Krochmal 2002).

15. Page 12, 2nd paragraph, 1st sentence: as said before, this is not true, given that scavenging may indirectly affect herbivore populations and thus carrion availability (see Molen et al. 2014 Biol. Rev.).

We have removed the part of the sentence where we mistakenly suggest that scavengers cannot affect carrion availability.

16. Page 13, 3rd and 4th sentences: whaling has exerted also a huge negative impact on scavengers by depleting whale populations. If you are going to talk about human impacts, maybe is better to do it at the end of the ms, perhaps in a new section in which you explore which scavenging traits could be more

successful in a human dominated world.

This has been removed.

17. You should also take into account facilitative processes. For instance, some scavengers are able to access the interior of carcasses only once other, more powerful species, has opened the skin (see Molen et al. 2014 Biol. Rev.).

18. Page 14, bottom paragraph, 2nd sentence: Id change it to This is true for many vultures and other major avian scavengers such as albatrosses who all have [].

We have reworded the sentence as suggested.

#### FOOD PROCESSING

19. Page 16, 2nd paragraph, 6th sentence: insert Within mammals, before This ability.

This has been added.

20. Page 17, 2nd paragraph, 4th sentence: do you refer to species or individuals? Higher species diversity doesnt mean more individuals.

The reference of Pobiner (2015) states that there were more individuals and we have changed the sentence to reflect this.

21. Page 18, 1st sentence: change enabling to enable.

This has been changed.

22. Page 18, 3rd sentence: thus? I dont understand this sentence; could you please reword it?

We have reworded this sentence. The idea is that early birds didn't have beaks and so could more easily eat meat. This is in contrast to modern birds where a beak may be a hindrance.

23. Page 18, 5th sentence: The mix of strong and weak features in their skull morphology; please explain it.

#### CONCLUSION

24. Page 18, bottom paragraph, 3rd sentence: change technique to approach?

This has been changed.

#### FIGURES

25. Fig. 2: you may insert the name and Mya range of each period in the X axis rather than in the figure legend. Also, Id indicate aerial, terrestrial and aquatic in the Y axis rather than in the legend.

Hope this helps, Marcos Molen

Yours Sincerely,  
Adam Kane and co-authors