

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. For improved clarity in this document and in the manuscript, we have highlighted our responses in [blue](#).

1 Recommendation by the Subject Editor (anonymous):

Three experienced reviews have evaluated your manuscript. Two of them are extremely critical of several aspects related to the general handcraft and novelty of the review. The third reviewer is more positive, while making substantial recommendations for improvement of the manuscript. Should you be able to address all of the reviewers comments in a much revised version of the manuscript I would happy to reconsider the manuscript for consideration in *Ecography* and the E4 Award. This is not a provisional acceptance, since the manuscript would need to be revised again.

[As we note below, we feel our earlier manuscript did not capture the hierarchy we had in mind. This updated version is more explicit in terms of the structure where we now highlight the sections and subsections. Regarding the novelty of our manuscript, we have changed our introduction which was too similar to deValult et al. \(2003\) and no longer rely as heavily on the work of Beasley et al. \(2015\).](#)

2 Reviewer: 1

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 hap-

hazard 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 DeVault’s (2003) review paper on scavenging. In fact, there is almost nothing new here that is not covered in that earlier review.

We rewrote the introduction to reflect more accurately the aim of this 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?

We now specify the approaches we have in mind: “*e.g. energetics models, comparative anatomy, palaeontology etc.*”

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”.

We do not consider a binary response to scavenging behavior (i.e. facultative/obligate) and argue that all carnivorous vertebrates are placed along a gradient of scavenging. We state this more clearly in the introduction: “*there is no discrete divide between predators and scavengers but rather a continuous gradient (Pereira et al. 2014)*”.

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).

We have included this reference and explicitly discuss how differences in the physical properties of water Vs air can affect scavenging: *“The physical differences between water and air mean carcass availability is radically different between these environments (Beasley et al. 2012). For one, carcasses get moved around by water which results in a more diffuse signal being produced for would-be scavengers. Carcasses also tend to sink in water where they are no longer accessible to pelagic scavengers (Beasley et al. 2012). Research has shown that an animal need only travel between 16 to 36 km to encounter a fresh whale carcass (Molen and Snchez-Zapata 2015). The phenomenon of occasional bounties of carrion in the form of these whale falls has led some researchers to investigate if an obligate scavenger could survive by seeking out these remains exclusively.”*

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 hyena’s diet, but your text seems misleading. Most studies have shown that most of a hyena’s 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).

We have clarified this point about hyenas to say it is their ability to take large proportions of carrion under certain circumstances that makes them a useful focal species: *“The particular ability of hyenas to subsist on high proportions of carrion means we can use them as examples of efficient terrestrial scavengers to compare with other forms.”*

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

The hierarchy of our paper wasn’t clear in the first version but we have now clarified that this is the lead in to a larger section which has subsections e.g. food processing

3 Reviewer: 2

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.

One of the central points of our paper is to compare the biology of extant scavengers with extinct species in order to determine if they were suited to scavenging. All of the examples we use are backed up by references from previous work. Rather than taking them as fact we offer these as possible behaviours that the extinct species engaged in. Because we can’t observe their behaviour directly we are left to make assumptions about how likely they were to have engaged in them. But this is hardly unique to our work. We have added some extra references in support of our claims: *“Thus, given pterosaurs seem to have cohabited in large numbers (Witton 2013), and the known benefits this can have for social foraging in birds (Dermody et al. 2011), it seems probable that scrounging behaviours were seen in the flying pterosaurs as well.”*

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 certainly true that facultative scavengers can be variable in the proportion of carrion they consume but we would argue that species like hyenas have certain characteristics that make this possible. In contrast, cheetahs do not have a biology that lends itself to scavenging in the wild, due to poor competitive ability etc. We appreciate that there is a continuum across and among species which we specifically note in this revised version.

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 https://www.jstor.org/stable/20627167?seq=1#page_scan_tab_contents.

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.

The sections of Beasley et al. (2015) are the evolution of scavengers, competition between scavengers and environmental effects on scavenger ecology. These are very broad areas so in a review of this sort some overlap is inevitable. We feel our emphasis on extinct species and systems as well as

the frame of optimal foraging theory is a novel approach.

4 Reviewer: 3

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).

4.1 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 “in vertebrates” 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).

We changed the title of the manuscript to “A Recipe for Scavenging in Vertebrates - the natural history of a behaviour”.

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'd 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.

We clarified the structure of the manuscript by introducing clearer hierarchical subsections.

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), Cortés-Avizanda et al. (2012 *Ecology* 93:2570-2579), Cortés-Avizanda et al. (2014 *Ecology* 95:1799-1808), Moleón et al. (2014 *Biol. Rev.* 89:1042-1054), Pereira et al. (2014 *Mammal Rev.* 44:44-55), Périquet et al. (2015 *Biol. Rev.* 90:1197-1214), Mateo-Tomás et al. (2015 *Divers. Distrib.* 21:913-924), Moleón & Sánchez-Zapata (2015 *BioScience* 65:1003-1010), Moreno-Opo et al. (2016 *Behav. Ecol.*), Sebastián-González 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 Moleón & Sánchez-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: Moleón & Sánchez-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 Périquet 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 Moleón et al. 2014 *Biol. Rev.*).

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

Page 5, bottom paragraph, 1st sentence: Mateo-Tomás et al. (2015) is more general than Kendall (2013).

Page 8, 1st and 2nd sentences: see Pereira et al. (2014) and Périquet 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 Moleón 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 Cortés-Avizanda et al. (2014) instead.

Page 14, 2nd paragraph, 1st sentence: see also Moleón et al. (2014 Biol. Rev.) and Pereira et al. (2014).

Page 14, 2nd paragraph, 2nd sentence: see better Pereira et al. (2014) and Périquet 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 Moleón 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 Moleón et al. 2015).

4.2 Minor comments:

1. GENERAL: Please provide line numbers to facilitate the reviewing process.
[Line numbers have now been included.](#)
2. ABSTRACT: You could remove “, the first to our knowledge”.
[This has been removed.](#)
3. ABSTRACT: Also, you could mention some relevant specific findings of your synthesis.
4. THE CHALLENGES OF SCAVENGING: 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).
5. ENCOUNTER RATE: Page 3, bottom paragraph, 3rd line: change “Alternatively” to “Also”?
[This has been changed.](#)
6. METABOLISM: Page 4, 1st sentence: “the sporadic nature of carrion”; please explain.
7. LOCOMOTION: Page 4, bottom paragraph, 1st sentence: change “inherent” to “relative”.
[This has been changed.](#)
8. LOCOMOTION: Page 4, bottom paragraph, 3rd sentence: remove “, paradoxically,”.
[This has been deleted.](#)
9. LOCOMOTION: Page 5, 2nd paragraph, 1st sentence: change “appear” to “appeared”. Also, specify Mya for the Cretaceous period.
[This has been changed.](#)
10. LOCOMOTION: 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.

11. DETECTION: 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. DETECTION: Page 11, last sentence: explain why wind speed affects the olfactory capacity of an aquatic species.
13. PREY AVAILABILITY: I'd change this title to "Carcass Availability", which is more specific.

This has been changed.

14. PREY AVAILABILITY: 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 Cortés-Avizanda et al. 2012) and carcass accessibility (e.g., see DeVault & Krochmal 2002).
15. PREY AVAILABILITY: 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 Moleón et al. 2014 Biol. Rev.).

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

16. PREY AVAILABILITY: 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.

We have decided to remove this section because we felt human impacts go beyond the scope of our paper.

17. PREY AVAILABILITY: 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 Moleón et al. 2014 Biol. Rev.).
18. PREY AVAILABILITY: Page 14, bottom paragraph, 2nd sentence: I'd 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.](#)
19. FOOD PROCESSING: Page 16, 2nd paragraph, 6th sentence: insert "Within mammals," before "This ability".
[This has been added.](#)
20. FOOD PROCESSING: Page 17, 2nd paragraph, 4th sentence: do you refer to species or individuals? Higher species diversity doesn't mean more individuals.
[The reference of Pobiner \(2015\) states that there were more individuals and we have changed the sentence to reflect this.](#)
21. FOOD PROCESSING: Page 18, 1st sentence: change "enabling" to "enable".
[This has been changed.](#)
22. FOOD PROCESSING: Page 18, 3rd sentence: "thus"? I don't 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. FOOD PROCESSING: Page 18, 5th sentence: "The mix of strong and weak features in their skull morphology"; please explain it.
24. CONCLUSION: Page 18, bottom paragraph, 3rd sentence: change "technique" to "approach"?
[This has been changed.](#)

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

Hope this helps, Marcos Moleón

Yours Sincerely,
Adam Kane and co-authors