

Mummified cave cheetahs inform rewilding actions in Saudi Arabia

Corresponding Author: Mr Ahmed BOUG

This file contains all editorial decision letters in order by version, followed by all author rebuttals in order by version.

Attachments originally included by the reviewers as part of their assessment can be found at the end of this file.

Version 0:

Decision Letter:

**** Please ensure you delete the link to your author home page in this e-mail if you wish to forward it to your coauthors ****

Dear Mr BOUG,

Your manuscript titled "Mummified cave Cheetah inform rewilding actions in Saudi Arabia" has now been seen by our reviewers, whose comments appear below. In light of their advice we are delighted to say that we are happy, in principle, to publish a suitably revised version in Communications Earth & Environment.

We therefore invite you to revise your paper one last time to address the remaining concerns of our reviewers. At the same time we ask that you edit your manuscript to comply with our format requirements and to maximise the accessibility and therefore the impact of your work.

EDITORIAL REQUESTS:

Please review our specific editorial comments and requests regarding your manuscript in the attached "Editorial Requests Table".

We suggest that you submit a version of Fig. 3e or similar photos for use as feature images; please refer to our Editorial Requests Table for more details.

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We hope to hear from you within two weeks; please let us know if you need more time.

Best regards,

Heike Langenberg, PhD
Chief Editor
Communications Earth & Environment
Communications Sustainability

On Bluesky:
@commsearth.nature.com
@commssustain.nature.com

REVIEWERS' COMMENTS:

Reviewer #1 (Remarks to the Author):

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What is more suitable would be: "Ancient remains found in caves give insight to the evolutionary history of cheetahs in a natural hybrid zone in Saudi Arabia" (or something to that extent). Note that I say remains here, because you don't only analyse mummies but also skeletons.

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136. It needs to explained better why you picked only 7 or 3 (not quite sure) remains out of 54.

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141. Rephrase to: We followed the ANGSD pipeline designed for samples with low sequencing depth, during which we retained 23,000 single polymorphisms (SNPs), or which 7,000 were transversions.

It might also be worth explaining why you separate the two; it's fairly uncommon I think

Lastly: same as the comment above: 23,000 SNPs is not a full genome.

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157. The phylogenetic tree is quite unusual. I can't really tell genetic distances apart - perhaps it'd be better to just go for a classic NJtree?

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Perhaps structure the Results / Discussion as following: (1) how and where the caves were found; (2) how many caves contained animal remains and how many of those were cheetah (a supplementary table would be useful), (3) age calibrations of the 7 remains (explaining why only these were chosen) to find out the era in which they lived; (4) skull measurements, to infer the age of the specimens (to tell you something about their ecology – did cheetah slip in and fall, or could caves have been used for shelter and raising their cubs?), (5) genome sequencing to infer their genetic relations to surrounding cheetah populations.

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191. This sentence is not interesting for your study. What's interesting is whether your findings suggest that Arabian cheetahs may also have been using the caves as denning sites. If there were really that many in comparison to prey (I'm still not sure what their proportions were) – then it would be likely. If many were cubs, it would be even likelier. I doubt that cheetahs would fall into these caves more easily than their prey; yet, they are more likely to climb out

194. You should talk about carbon dating directly after you show your carbon data (hence, in the paragraph) because results & discussion are combined in this journal. More importantly: carbon dating / skull scanning / genome sequencing weren't really needed to illustrate the long term presence of cheetahs, just finding their remains was enough. You should discuss these results separately and highlight their value, i.e. the new insights that you got.

210. Hmm.. so here it sounds like the proportion of cheetahs was actually very low. Not a "cheetah cave" after all.

Methods:

The methods, unlike the Results&Discussion, are very clear and well written.

445. Figure 1 makes it appear that there was one location with only mummies. But gathering from the manuscript, there were 5 different caves that contained cheetah remains, including skeletons?

Reviewer #2 (Remarks to the Author):

I would like to begin by congratulating the authors for an exceptional and truly groundbreaking piece of work. The manuscript presents a discovery that, in my opinion, represents a milestone in the study of carnivore paleoecology and conservation biology: the finding of both skeletal and naturally mummified cheetah remains within karstic cave systems in Northern Saudi Arabia. This constitutes, to my knowledge, the first evidence of natural mummification in a large felid, and more specifically in *Acinonyx jubatus*. Such a result is of the utmost importance, not only for paleontology but also for conservation efforts, since it provides invaluable insights into the genetic composition and ecological history of cheetahs in Arabia.

The manuscript is well written, clearly structured, and of wide interdisciplinary interest. It combines paleontological data, radiocarbon chronology, taphonomic observations, and paleogenomics in a very compelling manner. The novelty and significance of the findings cannot be overstated: they will undoubtedly open new perspectives for rewilding initiatives in the region, especially regarding the choice of source populations for potential reintroduction programs.

One aspect that I find especially striking is the presence of cheetah remains in cave contexts. To my knowledge, no modern *Acinonyx* populations have ever been documented using caves as refuges, for denning, or for prey storage. The only somewhat comparable case, already stated by the authors, would be *Miracinonyx trumani* in North America, which is now considered closer to *Puma* and not directly to *Acinonyx* or the sabertoothed cat *Homotherium* in southern USA. In contrast, leopards are well known to have used caves extensively in the European Pleistocene, where they regularly employed them as refuges and dwelling sites (see Prat-Vericat et al., 2025, Quaternary Science Reviews). The discovery of cheetahs in caves in Arabia therefore raises important questions about behavioral plasticity and ecological adaptation of this species in the past. Although I understand that the primary focus of the manuscript is the presentation of the discovery itself and its genetic implications, I would strongly encourage the authors to add at least a short discussion on the potential ecological significance of this cave association. Even if speculative, it would highlight the possibility of behavioral patterns not documented in extant cheetah populations, and would enhance the broader ecological relevance of the findings.

In terms of presentation, I have a few minor suggestions that could strengthen the manuscript further:

Supplementary material – The impact of these extraordinary discoveries would benefit from additional photographic documentation, both of the mummified individuals and of the cave contexts. Similarly, a more detailed description of the geological and karstic framework would be useful, even if placed in supplementary materials, to provide readers with a clearer understanding of the depositional environment.

Ecological framing – As mentioned above, including a few sentences on the ecological implications of cheetahs being preserved in caves (and how this contrasts with extant cheetah ecology) would add a very valuable perspective.

Conservation perspective – The manuscript already emphasizes the implications for rewilding. It may be worth underlining more explicitly how these findings demonstrate the potential of paleontological data to inform present-day conservation management, especially in regions where baseline ecological information is scarce or has been lost due to historical extirpations.

Overall, however, these are relatively minor points. They do not detract from the fact that this is an outstanding contribution. The discovery of naturally mummified cheetahs in Arabia is of global importance and will attract considerable attention across disciplines, from paleontology and taphonomy to conservation biology and genetics.

Reviewer #3 (Remarks to the Author):

The manuscript titled "Mummified cave cheetah inform rewilding actions in Saudi Arabia" by Boug et al. integrates geochronological and paleogenetic data from mummified *Acinonyx jubatus* specimens found in karstic environments.

The manuscript presents very interesting and innovative scientific content. This study highlights the value of paleogenetic research as an important tool for conservation. The findings demonstrate that ancient specimens can provide valuable genetic data, which is fundamental for decision-making in rewilding programs. The methodology employed is appropriate for the study's objectives and was presented in a clear and detailed manner. Nevertheless, it requires minor modifications prior to acceptance for publication.

I suggest a change to the title of the topic "Radiographic analysis of cheetah skull morphologies," as the section also addresses geochronological aspects. A more comprehensive and accurate title that reflects both themes would be more appropriate.

This study demonstrates enormous potential for providing theoretical and practical support for the design and implementation of rewilding plans. Therefore, it is suggested that the authors expand the discussion on this topic, detailing the applicability of the generated data in guiding and fostering ecological restoration actions. This information can be integrated at the end of the "Results and Discussion" section, expanding the concluding paragraph, or, alternatively, included in a specific "Final Considerations" section to lend greater visibility to the work's relevance for biodiversity conservation. This will strengthen the study's conclusions.

The figure numbering requires correction. Figure 2 is being referenced in the text as Figure 3.

It's important that the authors revise the reference list. There are discrepancies between in-text citations and the final bibliography, such as references that appear in the text but are not included in the list, as well as publication dates that differ.

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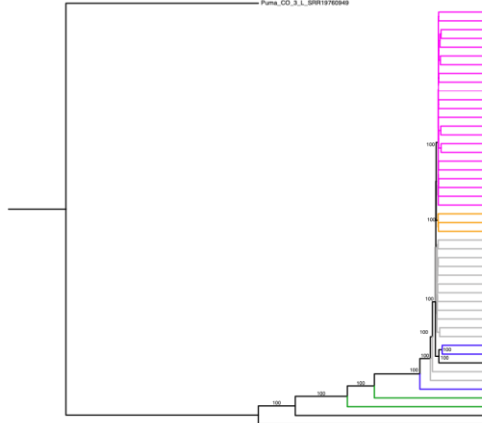
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Furthermore, I don't think rewilding should be the main aim of your research, because it makes it sound like it is driven by a hidden agenda (say, to release African cheetahs into Saudi Arabia). The conservation implications are definitely important, and I don't disagree with the conclusions drawn, but it can best be discussed in a separate paragraph in the Discussion. At the end of the introduction, you can say something like: "Based on our discoveries, we further discuss recommendations for conservation management with regards to rewilding efforts currently being undertaken in Saudi Arabia."	Thank you for your comment. We agree with this suggestion and have revised the Introduction and Discussion to clarify that rewilding is discussed as a conservation implication rather than a primary research aim. We have also added the suggested sentence (Based on our discoveries, we further discuss recommendations for conservation management with regards to rewilding efforts currently being undertaken in Saudi Arabia.) at the end of introduction.
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Abstract: The Abstract misses a research aim / questions and a Method section.	Thank you for pointing this out. Research aim and method section was added to abstract.
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47. Like before-mentioned: informing conservation measures is nice, but perhaps it shouldn't be the immediate aim of this study. It makes it appear like there is a second agenda, which raises the suspicion of potential research bias. Rather, I would say that the study / mummies allow a unique peak into the evolutionary history of cheetahs, which is of particular interest because the area may have formed a natural hybrid zone between two subspecies. You can of course mention the rewilding efforts, and draw conclusions from your results. But you have to be careful to not make it sound like you already had the conclusion in mind before you even started the study - a particularly sensitive issue with cheetahs relocations as of late.	Thank you for the comment. The immediate aims of the study have been added to the introduction as suggested by your previous comment. Further conclusion at the end of the manuscript elaborated more on the conservation management implications of this study.
49. one genome sequence of 7 cheetahs?	Sentence was reframed to clarify.
53. Asian cheetah should be Asiatic cheetah: please correct throughout the manuscript Introduction:	Thank you. This was corrected.
59. 'great felid species' is pretty unusual. People normally say big cats, or large felids. This sentence also needs a reference	Thank you. This was corrected and reference added.
62. This sentence needs to be rephrased, because now it sounds like cheetahs are only left in Iran. It's important to mention how many subspecies there are and how many are left in Africa and Asia, to put things in perspective.	Thank you. The sentence was rephrased and suggested information added.
64. Start sentence with: "In the Arabian Peninsula, the last records occurred..."	Thank you. This was corrected.
76. I had to look up what coursing meant and read online that "the sport of hunting game animals such as hares with greyhounds using sight rather than scent". So maybe say game hunting, not to confuse the reader? But I might be wrong, and this may be an official term	Thank you. This was corrected.
77-80. This statement doesn't make much sense. Agriculture started thousands of years ago, whereas cheetahs only went extinct in the past century. Some carnivores (like caracals and ocelots) even thrive around agricultural fields, because the number of small rodents explode. Cheetahs were simply captured and poached to extinction, and quite recently it seems.	Thank you. This statement was removed.

82-86. This sentence is as chaotic as it is unclear. (and rewilding is not with a capital)	Thank you. The sentence was reframed.
86. I would say this is Discussion material. Likewise, a lot of information in the Discussion should go to the Introduction. Because now, the emphasis lies heavily on releasing cheetahs back into the area, but I still don't know how you got the cheetahs mummies and why you decided to analyze them.	Thanks for the comment. The introduction and results sections were reframed and rearranged to clarify the conservation implications of this study.
91. Cheetah should not be with a capital. This sentence is also a repeat (we know that they went extinct already)	Thank you. The sentence was reframed.
93. Why is the Asiatic cheetah the obvious choice? I'm also pretty sure that Asiatic cheetahs are not being captive bred in Iran at the moment. What's more relevant is to mention that there are only a handful left; 12 individuals or so? It's impossible to source from this population.	Thank you for your comment. Critically low population of Asiatic cheetah was acknowledged.
94. How do you know the Peninsula is connected to the Africa cheetah population? To the African mainland, sure, but you don't yet know whether there was historical gene flow.	Thank you. This was removed.
96. Why captive breeding programmes? Why not get cheetahs from the wild?	Thanks for raising a critical question. Cheetahs of wild source might also be considered for future reintroduction programs besides rewilded captive bred cheetahs.
Results & Discussion: 104. You start with the walking distance to each cheetah, but we don't know anything about the number of caves and number of cheetahs yet. I would start with that	Thank you. This section was rephrased.
108. Here you say 20 skulls, but in the Table there are measurements of 30 cheetahs, and in the introduction you refer to 7 cheetahs?	Thank you for the comment. Table also contains details of 20 skulls and the first column represents IDs not the serial number. It is cleared now in the table heading.
110. What is the main cave?	It was renamed as cave 1.
111. You say "negligible (n<3)" but then list "significant gazelle remains (n=164)". Perhaps try to find a way to present the results more pragmatically, not to confuse the reader.	Thank you for the comment. This was rephrased to make it clear
117. So there are five cheetah caves, meaning that out of 134 caves you surveyed, only 5 contained cheetahs? If so, please clarify that in the beginning. Were there any animal remains found in the other caves? Because it's quite important in relation to your statement that caves were overused by cheetahs in comparison to	Thank you. This was corrected.

their prey.	
118. 05?	Corrected
119. The camera traps are new; and a bit of an unaccepted method tool. Because there were never any research questions / aims of this study, I don't quite know why you would place these. If you are only interested in guiding reintroductions, why put out camera traps for an extinct species? It again sounds a bit like "might as well". Likewise, why measure the skulls at all? What did you aim to find out?	Thank you for the comment. Camera trap information was removed and skull measurement study was justified in the text.
136. It needs to explained better why you picked only 7 or 3 (not quite sure) remains out of 54.	Thank you for the comment. This has been added in the text that a representative sample was taken to study dating and genetics of the skeletal remains and mummies.
You say "full mtDNA sequences", but I can see in the Figure that only 929 base pairs were sequenced – far from a full genome. It would be important to elaborate which part of the mitogenome this is: control region, cytochrome b etc. Its because some regions don't show much variation in species with low genetic diversity (such as cheetah) and are thus quite uninformative for telling apart subspecies. It would therefore also be important how many parsimony informative sites you found in your mtDNA alignment.	We generated full mitochondrial genomes, but the only widely sampled reference data set that is available (Prost et al. 2022) for comparison includes only 929b of mitochondrial DNA. We only refer to "mitochondrial DNA" not full mitochondrial genomes" when we talk about the phylogenetic network. We included the DNA regions used in the network in the captions. They were originally chosen as they are highly informative for the species.
141. Rephrase to: We followed the ANGSD pipeline designed for samples with low sequencing depth, during which we retained 23,000 single polymorphisms (SNPs), or which 7,000 were transversions.	We rephrased the text to "We obtained around 7,000 or 23,000 single nucleotide polymorphisms (SNPs) for phylogeographic analyses after filtering when including just transversions or both transitions and transversions, respectively. The former was used to avoid biases potentially arising from DNA damage in the ancient cheetah data, which commonly affects transversions (Briggs et al. 2007)."
It might also be worth explaining why you separate the two; it's fairly uncommon I think	We thank the reviewer for pointing this out. It is common in ancient DNA, but many reads will not be

	familiar with the field and so it is good to add information on this also here and not just in the Methods section. We added: “The former was used to avoid biases potentially arising from DNA damage in the ancient cheetah data, which commonly affects transversions (Briggs et al. 2007).”
Lastly: same as the comment above: 23,000 SNPs is not a full genome.	We sequenced whole genomes but only use 7,000 or 23,000 SNPs for the analyses, which is common in population genomic analyses. In these cases, we are referring to the data as genome-wide, but the fact remains that we generated whole genomes. Hope this clarifies the use of whole genome and genome-wide data in the text.
156. Cluster	Changed
157. The phylogenetic tree is quite unusual. I can't really tell genetic distances apart - perhaps it'd be better to just go for a classic NJtree?	The divergence times of cheetahs are very recent and together with recombination and ancient admixture these lead to reticulations in phylogenetic networks. However, standard phylogenetic methods are depicted as bifurcating trees, and thus not able, for example, to handle the presence of recombination. A bifurcating tree with such short branching times is not readable and does not provide reliable information. Here the bifurcating tree of the data:

	 We thus decided to use a phylogenetic network, which offers more information than a bifurcating tree.
168. It sounds like this should be the start of the introduction. Perhaps structure the Results / Discussion as following: (1) how and where the caves were found; (2) how many caves contained animal remains and how many of those were cheetah (a supplementary table would be useful), (3) age calibrations of the 7 remains (explaining why only these were chosen) to find out the era in which they lived; (4) skull measurements, to infer the age of the specimens (to tell you something about their ecology – did cheetah slip in and fall, or could caves have been used for shelter and raising their cubs?), (5) genome sequencing to infer their genetic relations to surrounding cheetah populations.	Thank you for the suggestion. The Results and discussion section has been rearranged to address the comment.
173. Rephrase:	Author's opinion is that this is a clear statement
176. This is a repeat	Author's opinion is that at this point this sentence gives a comparison with domestic cat mummification.
191. This sentence is not interesting for your study. What's interesting is whether your findings suggest that Arabian cheetahs may also have been using the caves as denning sites. If there were really that many in comparison to prey (I'm still not sure what their proportions were) – then it would be likely. If many were cubs, it would be even likelier. I doubt that cheetahs would fall into these caves more easily than their prey; yet, they are more likely to climb out	This part was rephrased and possibility of cheetah using caves as denning site was discussed.

194. You should talk about carbon dating directly after you show your carbon data (hence, in the paragraph) because results & discussion are combined in this journal. More importantly: carbon dating / skull scanning / genome sequencing weren't really needed to illustrate the long term presence of cheetahs, just finding their remains was enough. You should discuss these results separately and highlight their value, i.e. the new insights that you got.	Thank you for your comment. The carbon dating part was relocated as suggested. Carbon dating was done to gain insights about which subspecies was present in the region at what point of time. This is now clear from the text.
210. Hmm.. so here it sounds like the proportion of cheetahs was actually very low. Not a "cheetah cave" after all.	Thank you for pointing this out. The proportion of Cheetahs in each cave is now given clearly in the manuscript.
445. Figure 1 makes it appear that there was one location with only mummies. But gathering from the manuscript, there were 5 different caves that contained cheetah remains, including skeletons?	Thank you for your comment. An additional figure was added to show the location of caves.
Reviewer #2 (Remarks to the Author):	
Although I understand that the primary focus of the manuscript is the presentation of the discovery itself and its genetic implications, I would strongly encourage the authors to add at least a short discussion on the potential ecological significance of this cave association. Even if speculative, it would highlight the possibility of behavioral patterns not documented in extant cheetah populations, and would enhance the broader ecological relevance of the findings.	Thank you for the comment. The suggested information was added to the discussion section.
Supplementary material – The impact of these extraordinary discoveries would benefit from additional photographic documentation, both of the mummified individuals and of the cave contexts.	Thank you for the suggestion. Photographs were added as supplementary material to the paper.
Similarly, a more detailed description of the geological and karstic framework would be useful, even if placed in supplementary materials, to provide readers with a clearer understanding of the depositional environment.	Thank you for the comment. Unfortunately this remote part of the country lacks information pertaining to the geological and environmental aspects.
Ecological framing – As mentioned above, including a few sentences on the ecological implications of cheetahs being preserved in caves (and how this contrasts with extant cheetah ecology) would add a very valuable perspective.	Thank you. This information was added to the results and discussion section.

Conservation perspective – The manuscript already emphasizes the implications for rewilding. It may be worth underlining more explicitly how these findings demonstrate the potential of paleontological data to inform present-day conservation management, especially in regions where baseline ecological information is scarce or has been lost due to historical extirpations.	Thank you very much for the comment. Following information was added at the end of discussion section: The integration of paleontological and genomic data from the cheetah remains provide a rare opportunity to bridge historical ecology with present-day conservation planning. These findings demonstrate how ancient DNA records can reconstruct lost baseline of species distribution, genetic diversity, and ecological associations which form the critical information for developing evidence-based rewilding and restoration programs. In regions such as the Arabian Peninsula, where historical faunal baselines were erased by millennia of climatic shifts and human pressures, the identification of past cheetah lineages offers valuable reference points for genetic sourcing and feasibility assessments of future reintroduction initiatives.
Reviewer #3 (Remarks to the Author): I suggest a change to the title of the topic "Radiographic analysis of cheetah skull morphologies," as the section also addresses geochronological aspects. A more comprehensive and accurate title that reflects both themes would be more appropriate.	Thank you for the comment. The sections were separated and renamed as suggested.
This study demonstrates enormous potential for providing theoretical and practical support for the design and implementation of rewilding plans. Therefore, it is suggested that the authors expand the discussion on this topic, detailing the applicability of the generated data in guiding and fostering ecological restoration actions. This information can be integrated at the end of the "Results and Discussion" section, expanding the concluding paragraph, or, alternatively, included in a specific "Final Considerations" section to lend greater visibility to the work's relevance for biodiversity conservation. This will strengthen the study's conclusions.	Thank you for the comment. The applicability of the this study in guiding and fostering ecological restoration actions was added to the discussion section: The integration of paleontological and genomic data from the cheetah remains provide a rare opportunity to bridge historical ecology with present-day conservation planning. These findings demonstrate how ancient DNA records can reconstruct lost baseline of species distribution, genetic diversity, and ecological associations which form the critical information for developing evidence-based rewilding and restoration programs. In regions such as the Arabian Peninsula,

	where historical faunal baselines were erased by millennia of climatic shifts and human pressures, the identification of past cheetah lineages offers valuable reference points for genetic sourcing and feasibility assessments of future reintroduction initiatives.
Figure 2 is being referenced in the text as Figure 3. -	Thank you for pointing this out. This has been corrected.