Peer review history for:

Ramello V, Monti IE, Sogliani D, Le Roux L, Isaja V, Muzuma U, et al. Spatio-temporal behaviour of the brown hyena (*Parahyaena brunnea*) in the Fish River Canyon, Namibia. S Afr J Sci. 2025;121(11/12), Art. #20710. https://doi.org/10.17159/sajs.2025/20710

HOW TO CITE:
Spatio-temporal behaviour of the brown hyena (*Parahyaena brunnea*) in the Fish River Canyon, Namibia [peer review history]. S Afr J Sci. 2025;121(11/12), Art. #20710. https://doi.org/10.17159/sajs.2025/20710/peerreview

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Reviewer 1: Round 1
Date completed: 17 March 2025
Conflicts of interest: None

Recommendation: Accept / Revisions required / Resubmit for review / Resubmit elsewhere / Decline / See comments
REVIEWER: Revisions required
With regard to our policy on 'Publishing peer review reports', do you give us permission to publish your anonymised peer review report alongside the authors' response, as a supplementary file to the published article? Publication is voluntary and only with permission from both yourself and the author. Yes/No
REVIEWER: Yes

Comments to the Author:
I think this is a nice paper and a good addition to the literature, as first study of this type about brown hyenas in the Fish River canyon.

Overall, I think it is nicely written. However, some sentences are not very clear and could be rephrased. The author must also make sure to use either US or UK English (as per the journal guidelines), as there is a mix of both throughout the manuscript.

I also think that a little bit more information background about the area would benefit the paper, to explain the context better to the reader. For example, describe the presence of water (or not) and the prey species present in the area. Indicating the temperatures and rainfalls could also be interesting. I assume that the temperatures can vary a lot depending on the season and potentially influence brown hyena activity patterns.

[See Appendix 1 for Reviewer 1's comments made directly on the manuscript]

Author response to Reviewer 1: Round 1

"Strictly" is a strong word. Brown hyenas are indeed mostly nocturnal, but they can be active during the day in some contexts. I would find another word.

AUTHOR: Line 2: Thank you for your suggestion. We have removed the word "strictly" to better reflect the intended meaning and to avoid overstating the behaviour described.

Also, we decided to implement the Methods for the classification of the species as cathemeral, diurnal, nocturnal, and crepuscular following the recent paper published by Gerber et al. (2024) that allows for standardisation of diel phenotypes classification. By refining our methodology for calculating with much

more precision sunset, sunrise, start of the night, and end of the night values, as well as crepuscular hours (twilight), we now present a highly precise classification. Accordingly, the brown hyena is now categorised as 'cathemeral', with 22.6% and 64.5% of detections at daytime and nighttime, respectively. We corrected both the Methods and the Results sections to take into account these changes.
US English here but UK English before. Both languages were used throughout the manuscript. Be consistent.
AUTHOR: We appreciate the reviewer's careful reading. We have thoroughly reviewed the manuscript and implemented the necessary corrections accordingly.
Same comment as above about "strictly nocturnal". See Lemerle MA, …
AUTHOR: Line 41: Thank you for this insightful suggestion. In response, we have revised the wording in the text by removing the term "strictly" to more accurately reflect the potential for diurnal behaviour.
Can you elaborate on this? Why are the studies controversial? Or do you mean that both authors have observed opposite things?
AUTHOR: Line 53-54: Thank you for highlighting this point. We agree that the phrase lacked clarity and, to avoid potential misinterpretation—particularly the implication that previous authors dispute the scavenging role of hyenas—we have decided to remove this statement from the manuscript. The controversial referred to the different findings in literature to define the relationship between brown hyenas and other large predators as well as the ability of the species to hunt.
I think it would be good to elaborate on the loss of brown hyenas in the eastern regions. Did they go extinct? When? Do we know what the population was previously (resident groups or just transient animals? Densities?)? Give more details about this. "recent years" is also not precise enough.
AUTHOR: Line 62-65: We appreciate the reviewer's helpful suggestion and acknowledge that this information could enhance the clarity of the paragraph. However, we have opted to remove the phrase *"Here the species has not been recorded in recent years, likely due to the heightened conflict with small–stock livestock farmers"*, as elaborating further would significantly increase the word count and the information is not essential to the core objectives of the study.
Also, the link is not very clear between "understanding the spatial ecology" and the dispersion to the East. Can you be more precise about how the results from your study will contribute to the repopulation of brown hyenas in the eastern regions?
AUTHOR: Line 67-68: Thank you for this constructive suggestion. We have expanded the discussion by linking the increased understanding of the spatial and temporal ecology of brown hyenas to potential conservation management strategies. This addition highlights how such knowledge can support efforts to address the specific ecological requirements of the species within the study area.
Are leopards the only co-occurring large predators? And springboks and hares the only prey? You wrote predators in plural but only cite leopards. Did you mean e.g. instead of i.e.? Maybe this is mentioned later, but it would be interesting to have a bigger picture of what species are present in the area.
AUTHOR: Line 70-71: Thank you for your observation. We have revised the wording to clarify that our analysis considered only leopards. A broader overview of the species composition in the study area is provided in the Materials and Methods section and in the Supplementary material. Additionally, we have included an explanation for our selection of the two prey species, which also addresses a related comment raised by another reviewer.
I would start directly at "we predicted that…" and remove the first part of the sentence. You explain the ecological role in the following sentence.
AUTHOR: Line 74: Thank you for the suggestion. We have implemented the recommended change as advised.
Due to conflict on the neighbouring farms?
AUTHOR: Line 107: Thank you for pointing this out. The eradication of larger predators was indeed the result of multiple factors, including direct persecution through hunting and indirect effects related to the predominant land-use practices—specifically small-stock farming—until the mid-1990s (see Brown, 2006). We have added a clarifying sentence to the manuscript to better reflect this understanding.
When? In 1995?
AUTHOR: Line 111-112: Thank you for this helpful observation. The recovery has been observed following the establishment of several private reserves surrounding the national park, collectively forming the

Greater Fish River Canyon Landscape (GFRCL). As comprehensive information on the establishment dates of all individual areas is not available, we have revised the sentence to specify that the recovery has occurred since the formation of multiple protected areas that now constitute the GFRCL.
Nice, this answers my comment from above. Can you maybe also cite the main prey species present?
AUTHOR: Line 107-116: Thank you for your suggestion. We have included the requested information in the supplementary material, as incorporating it into the main text would have significantly increased the word count, which is already constrained by the manuscript's length limitations.
Why 5 minutes? Studies sometimes use 1 min interval. Do you have a reference for that?
AUTHOR: Dear reviewer, thank you for this question. A 5-minutes delay enhance independent detections as it reduces the possibility that the same animal is detected in front of the camera-traps. Additionally, it preserves the data-storage capacity of the camera-traps external memory. To our knowledge, most studies and colleagues use a 1-to-5 min delay between triggers. This delay revealed to be ideal for a diversity of mammalian species: https://doi.org/10.1071/WR17181
Compared to your list of present carnivores above, can you elaborate a bit more why you only chose to include leopards in your analysis (why not cheetahs for example)? You can also do the same for prey species.
AUTHOR: The main reason for including only leopards in our analysis of predator interactions is that interference competition, particularly within predator guilds, is most likely to occur among carnivores of comparable body size, as noted in previous literature. Consequently, we excluded mesopredators such as *Mellivora capensis* and *Vulpes chama* from our analysis, as their ecological interactions with brown hyenas are likely to be limited or asymmetrical. That said, we fully agree that exploring the temporal ecology of brown hyenas in sympatry with cheetahs would be of great interest. However, the extremely low number of cheetah detections in our dataset (n = 3), as well as similarly low detection rates for several other species listed in Supplementary Table 2, prevented us from conducting meaningful analyses for these taxa. In some cases, such as the cheetah, the very low RAI (0.06) may reflect a low local density and, consequently, limited temporal or spatial overlap with other carnivores, including the brown hyena. We acknowledge the importance of these potential interactions and suggest that further studies - some of which are already underway - should specifically target these low-density species to better understand their temporal and ecological dynamics in this landscape.
I am not sure that this table is necessary. It is redundant with the last paragraph of your introduction. If you have results that differ from your hypotheses, you can mention it directly in the discussion.
AUTHOR: Thank you for your thoughtful comment. We appreciate your perspective and see the value in your suggestion. However, this view contrasts with that of another reviewer who specifically appreciated the explanatory nature of the table. At this stage, we have chosen to retain the table, as we believe it provides a clear and concise summary of the rationale behind our covariate selection, which may be particularly useful for readers. To address your concern, we have enriched the table with additional explanation to provide deeper insight into our choices. We feel that incorporating all of this information into the main text would significantly increase the word count and potentially reduce the readability of the manuscript. That said, we remain open to removing or reformatting the table in a future revision, should it be deemed necessary during the next round of review.
SE?
AUTHOR: Line 233: It was. However, we removed this sentence because the calculation included all camera traps—including paired units—which lowered the average, as the double cameras were deployed later in the study. Since camera sites are considered as single units regardless of the number of devices, we felt this detail could be misleading and not particularly informative for the reader.
I like this table because it gives a good idea of the species present in the area
AUTHOR: Thank you.
You did not discuss this result in the discussion.

AUTHOR: Thank you for pointing this out. You are correct—the result in question was not discussed in the Discussion section. This was a deliberate choice, as the covariate related to sampling effort was included primarily as a control variable to assess whether the duration of camera trap deployment influenced detection probability, rather than as a key ecological factor of interest.

The negative effect observed was indeed unexpected, as sampling effort typically has a positive or neutral influence on detection probability. We believe this result likely reflects the ecological context of our study: the very low density of brown hyenas combined with a relatively high number of non-detections. In such settings, increased effort does not necessarily lead to higher detection but may instead accumulate additional non-detection events, producing a statistical association that appears negative.

Given the auxiliary nature of this covariate and its limited relevance to our core research questions, we chose not to include it in the Discussion. However, we acknowledge that the result is noteworthy and appreciate your attention to it.

You did not explain the cumulative weight model in the method section. I think it is great that you included it, so it would help the reader to understand what the cumulative weight means.

AUTHOR: 200-203: Thank you for your helpful comment. You are right—we did not include a description of cumulative model weights in the Methods section. We appreciate your observation and agree that providing a brief explanation would help readers unfamiliar with the concept better interpret the results.

Cumulative model weights are a useful summary in model selection procedures, as they reflect the total Akaike weight of all models in which a given covariate appears, offering an indication of the overall support for that covariate across the candidate model set.

While we did not include a formal explanation in the Methods section in the current version of the manuscript, we have added a concise description in the revision to improve clarity and accessibility for readers less familiar with this approach.

It would be interesting to have a note about where can the water be found. Is there only water in the main canyon, or can you also find some in the secondary ones? I know that your models did not seem to show an influence for TWI, but I think it would be worth indicating the presence of water or not.

AUTHOR: Line 309-315: Thank you for this valuable suggestion. We added a few sentences in the discussion to highlight water availability and distribution in the study area, both natural and artificial. Within CNP water is found sparsely both on the plateau and the canyon. The plateau has a number of artificial waterholes that guarantee year-round water accessibility to the species in the area. In the canyon water is found mainly along the Fish River itself where some ponds retain water even during the dry season, and in natural springs. Mapping natural water points is challenging. The TWI was mainly included to reflect the presence of drainage lines that could aid animal movements. We did not expect a role of water on the species' spatial ecology as it is reported in literature that brown hyenas are independent from it. However, it has been reported that they do drink when water is available. We reserve future studies to investigate the possible role of water accessibility on the species ecology.

It feels like a word is missing here. "influence brown hyena presence?"

AUTHOR: Thank you for your suggestion. We have incorporated the term "spatial ecology" into the text to improve clarity and precision.

Related to my previous comment. If there is no water on the plateau, do you think that brown hyenas often go down the canyon to drink water? Which could also explain the high detection rate in the secondary canyons? The covariate TWI was removed from the main model but I wonder if it would still be worth analysing anyway? Maybe separately?

AUTHOR: Thank you for this valuable insight. Brown hyenas are generally considered to be independent of water sources; however, they are known to drink when water is available. In our study area, water is present primarily at artificial water points on the plateau, while in the canyon it occurs more sparsely in natural springs, particularly during the dry season. These natural sources are difficult to map and quantify accurately.

For this reason, we did not include water accessibility as a covariate in our analysis of brown hyena spatial behaviour. Based on existing literature, water availability is not considered a key factor influencing the spatial ecology of the species. We therefore do not believe that brown hyenas actively roam in search of water. Instead, we hypothesise that secondary canyons are primarily used as travel corridors to access the plateau, where higher ungulate densities may offer better scavenging or hunting opportunities.

Nonetheless, we do have photographic evidence of brown hyenas at artificial waterholes, suggesting that they do make use of both artificial and natural water sources. While CNP is located in an arid region, the combination of permanent springs and strategically placed artificial waterholes ensures water availability throughout the year. Therefore, if would not be considered a limiting factor.

I feel like this sentence does not fit here. It is confusing. Make it clearer that this is something observed in other studies but not the case here.

AUTHOR: Line 359-363: We have clarified the concept by revising the wording of the relevant sentences to enhance clarity and readability.

In different foraging strategies?

AUTHOR: Line 374: Thank you for pointing this out. We have made the correction by changing “at” to “in” to ensure grammatical accuracy and improve the flow of the sentence.

I don’t really understand this sentence. When did hyenas change their behaviour? Do you mean that they change their behaviour depending on the presence/amount of other carnivores and therefore carcass availability?

AUTHOR: Line 381-385: Yes. We modified the sentence to clarify this point. We suggest that as carcasses left by other predators are few, hyenas might rely on other food sources such as carcasses of animals died of natural causes, or hunting.

Reviewer 2: Round 1
Date completed: 03 March 2025
Conflicts of interest: None

Recommendation:
Accept / Revisions required / Resubmit for review / Resubmit elsewhere / Decline / See comments

REVIEWER: Revisions required

With regard to our policy on ‘Publishing peer review reports’, do you give us permission to publish your anonymised peer review report alongside the authors’ response, as a supplementary file to the published article? Publication is voluntary and only with permission from both yourself and the author.
Yes/No

REVIEWER: Yes

Comments to the Author:
The study is well written, correctly designed and results well explained. The graphs and tables allow to any reader to understand the study. Some limitations of the study should be mentioned and explained to the reader. This includes the characteristic low samples sizes of desert environments which limit the analyses of comparing brown hyenas to leopards and not include cheetahs as coexisting carnivore and important food source provider. This does not allow to see the full picture explaining brown hyena activity patterns and authors justify it by mentioning brown hyena predatory behavior on leporids and other species. Brown hyena hunting is a rare behavior most common of coastal ecosystems where hyenas feed on seals. It is possible that brown hyenas do hunt in the study area but likely not enough to support their existence. I suggest to read and review the comments, detail the limitations of the study and carefully elaborate the discussion and conclusions.

Specific comments:
Line 5: Brown hyenas are not strictly nocturnal. In fact, when living in coastal habitats, they are quite diurnal and in the desert they can be also be crepuscular and be observed during the first hours of the day. Please rephrase this (remove strictly).

Line 6: There are quite some studies published on brown hyenas over the last decade, search brown hyena on researchgate.

Line 9: southern should not be with capital letter, please modify throughout the whole manuscript (line 20, 35, etc).

Line 15: I read this now in the abstract but it is likely in the manuscript also. It is important when mentioning how human activity impacts brown hyena occupancy and detection probability to specify to the reader the little human activity present in your study area and also the level of persecution of the species, both when describing the study area and also in the discussion, so readers can compare your results (and the degree of human activity and disturbances) to other study sites and make your study more relevant.

Line 17: Do hyenas prey in your study area or mainly scavenge? If you mention predatory behavior you should provide evidence of it, otherwise hyenas mostly scavenge and kleptoparasite with only usual predation recorded at seal colonies.

Line 21: In the southern Namib together with brown hyenas there are cheetahs, leopards and spotted hyenas (these ones occurring less than 150km from your study area but surely some individuals have been seen around). The only species missing are the lions and perhaps in some parts also spotted hyenas, if you mean these, please precise.

Significance: 22-28: Please add the information available for brown hyenas in other study sites (coastal deserts, Kalahari). Even if data is not available on occupancy, there is quite some information on activity patterns and thus it can be mentioned that in your study area hyenas live in a desert without lions and away from coastal weather with stable food availability (e.g. seals).

Lines 36 and 37. This statement is not correct and the reference does not belong to any data provided on this. Namibia has stable and widely distributed numbers of members of the Hyanidae family. Their numbers have even increased over the last decade. Please read the Red data book published for carnivores in Namibia. It is available free online.

Line 41: modify for 4,365 – 10,111 and split the long sentence in two.

Line 45: deemed stable. Yes that is correct thus you contradict what was written in line 36, see my comment about it (or clarify if I misunderstood).

Line 47: remove strictly as I mentioned before.

Line 48. What is being overlooked. Is there any word missing? Their?

Line 51: This is not correct as I mentioned before. There is recent literature in this last decade (but I do agree that could be better).

Lines 53 and 54: Please do a basic search in researchgate. Just search for brown hyena. You will find many papers published within the las decade.

Lines 55-56: please provide reference/s

Line 58: mention also kleptoparasitism

Lines 63-64 northern and central should not be capitalised

Line 65 change the second “its” for “their”

Lines 68-69: This is inaccurate: Please modify the reference for number 3 (red data book of Namibia) which is more updated than 4 (IUCN Red List) and you will see in the distribution map that it is not correct. Easternmost should not be capitalised. Also not east (line 71)

Line 71: I am unsure that they will disperse much into the east, but let's hope!

Line 76, remove the plural to other co-occuring predators if you only did it for the leopard. You also have cheetahs, caracals and black-backed jackals there. Why not also including Oryx, kudu and cheetahs? I am not suggesting you should do it, just curious why it did not happen. Not enough data? Then it must be explained otherwise your study lacks of interactions from hyenas with key species.

Line 83: I would be very surprised if brown hyenas hunt (regularly) in your study area and it would definitely worth publishing that. If you do not have evidence of it, you should rather write kleptoparasite instead of hunting.

Lines 84-87: Without yet reading the discussion, please ensure you mention the impact of high daily temperatures on wildlife and their activity patterns.

Line 99: South West should not be capitalised as well in the line 100 and 101.

Line 107: Add Atlas of Namibia (freely available online) as a reference

Line 110, northern also not capitalised

Line 112, you might also add elephants and rhinos (although they are in neighbouring reserves)

Line 119: you can also add slender mongoose

Line 137 change was for were

Line 150: is there a specific reason to choose 5 days over other different period (3 or 4 days)? Do you know how would this have affected your results?

Line 174: why choosing Leporidae over Oryx and Kudu? You are more likely to find hyenas scavenging on Oryx and Kudu predated by cheetah and leopard than on hares. The likelihood of hyenas living/hunting on hares is very reduced in this ecosystem, (in comparison to the Kalahari or other ecosystems with higher grassland biomass). I believe that if you look at the abundance of these species in your camera traps, the ungulates will also be more abundant (and have a much higher biomass). This is something that should be explained with detail in your discussion to justify the choice of species.

Line 226: remove capital letter to southern

Line 248: remove 'the' before brown

Line 249: Springbok without capital letter

Line 256: It is striking mentioning potential prey and no providing info on Oryx, Kudu and Zebra.

Lines 265 and 266: When mentioning human and vehicles, what type of activities were carrying the humans (tourists hiking, management park staff, researchers, others?), as well as vehicles? Please add info on this before the discussion.

Line 269 southern without capital letter S

Line 277: please add reference for arid environments (cite Ingrid Wiesel, red data book of Namibia (Hanssen et al.) or in the Kalahari from Gus Mills

Lines 280 to 288: Does elevation really affect brown hyenas? or is it rather where vegetation is found, thus prey, thus other carnivores (leopard and cheetahs) and therefore scavenging opportunities? I would like to see something like that discussed here. I miss some basic and valuable biological and field knowledge discussing here the results. E.g. Hyenas use mountains to den but also to spend the day and rest because they are protected from the competitors and humans. At night, they roam in the more vegetated areas and frequented by game when searching for scavenging opportunities. Where you find springbok, oryx, zebra, you will find hyenas at night, foraging. You could identify where you detect hyenas at which time to understand their movement patterns and therefore explain when they are detected at certain locations.

Detection probability is also influenced by where and how you deploy the camera traps and in some areas (riverbeds, valleys, mountain ridges), it is difficult to cover the landscape enough with camera traps to ensure every hyena will be photographed and some landscapes are more difficult to cover. Therefore, the landscape also plays a role, not only brown hyena ranging behavior. It would be good to mention the targeted locations to deploy the camera traps. All of this may seem obvious but worth to discuss (or at least part of it).

Line 290 southern without capital letter

Lines 291 to 296: well, I see here some of the thoughts I discussed in the paragraph above 😉

Line 297: sorry but I still stumble that there is no reference yet to other species such as cheetah, oryx, kudu and zebra.

Lines 307-308: Do you have any evidence of brown hyenas predating on leporids in your study area? As well as what part of their diet they contribute to? Are these thoughts mostly driven by other ecosystems such as the Kalahari where leporids have a much higher density? You surely have camera trap pictures of hyenas carrying food back to their dens, what prey items can you see? When you mention the likelihood of predator encounters, do you mean leopards and cheetahs or hyenas themselves? Please clarify.

Do you have data on springbok density in comparison to other species of ungulates? If so, this data could back up why you choose such species.

Line 327. The references are wrong. Number 54 matches with a cougar study not with brown hyena. I did not check the other references but the issue may be also found throughout the text if a reference/number shifted. Check it out.

It would be good to add some references from hyenas in other southern African ecosystems (Kalahari, coastal Namibia).

Line 335. The low RAI values of cheetahs and leopard depend highly on where you set the camera traps. They indeed must live a low densities but likely higher than your camera traps recorded, otherwise check for recaptures of territorial individuals, if you see few, this is indication that you struggle to capture them (which is normal in such landscape!). I would be careful with such statement. Brown hyenas do not hunt (usually) in the Namib desert and I know this via GPS movement data of hyenas, cheetahs, leopards and lions. Hyenas move more than cheetahs and leopards and this is the reason you may capture them more than these cats.

Line 338: What is the sample size you have to support this statement?

Line 340: Hyenas would chase off big leopard males and a coalition of cheetahs from their carcass and rarely would wait for them to finish off their meal.

Lines 341-344. Edwards et al. had a low sample size (which is common in the desert) and the other studies you compare to are in more mesic areas with much larger sample sizes. I would be careful to take such conclusions (that hyenas do not scavenge in your study area as much because of your findings on activity patterns).

Lines 348: I think that by not adding cheetahs, oryx, kudu and zebra, you are missing part of the picture. Cheetahs are more diurnal than leopards, cheetahs leave more food behind and are easier to drive away from their kills than leopards. The activity pattern you may see from the hyenas may be an overlap with both cheetahs and leopards to increase scavenging opportunities. I would like to see something like this in the discussion which would also mention the limitation of this study.

Lines 355 to 357. I repeat what I wrote above. The lack of data from other species here drives to such conclusions because you can't see the whole picture (missing activity patterns of other interacting species such as cheetahs and more ungulates), in my point of view incorrect. If you have data to back-up that hyenas hunt in your study area, you should present it but no study in Namibia reported hyenas hunting away from the seal colonies (also no observations to my knowledge from the whole research field community).

Lines 369-371: Which larger predators are being proposed to be reintroduced in the area? Do you have more information on this, then please develop.

Line 386. Table one. The information and the justification of the species is well displayed and comprehensive. I must say that in such complex ecosystem with multispecies occurring at low densities but highly competing for resources, to have a good understanding that enables you to interpret your results, you need to include more species within your analyses or mention such limitation in your study (already limited by the characteristic low sample sizes of arid environments) and a more careful interpretation of the results.

Line 411, figure 3. This is likely the more diurnal activity pattern I ever observed from leopards which is very surprising due to the high daily temperatures. Do you have any explanations for this? How many pictures/events support this? From May to October it covers the coldest months of the year, thus it may explain that leopards were more diurnal than expected. If the camera trap survey is done during the hottest months, I could potentially affect your results. I think this should be mentioned in your discussion.

References: double check that your refeences match with the numbers in the text.

Supplementary table 2: This table answers many of my questions. It is obvious that with only 3 cheetah detections, the species can't be included in the analyses. Please mention this in the text.

Author response to Reviewer 2: Round 1

Line 5: Brown hyenas are not strictly nocturnal. In fact, when living in coastal habitats, they are quite diurnal and in the desert they can be also be crepuscular and be observed during the first hours of the day. Please rephrase this (remove strictly).

AUTHOR: Thank you for your suggestion. We have removed the word "strictly" to better reflect the intended meaning and to avoid overstating the behaviour described.

Line 6: There are quite some studies published on brown hyenas over the last decade, search brown hyena on researchgate.

AUTHOR: Thank you for bringing this to our attention. It was not our intention to undervalue other recent studies. Our reference was specifically aimed at recent spatial ecology research, particularly on occupancy. However, we acknowledge that the wording could be misinterpreted as suggesting that no recent

publications exist on the species, which is not the case—as reflected by the numerous relevant studies we have cited. Since this point is not central to the objectives of our study and to avoid any potential misinterpretation, we have decided to remove the sentence both from this section and the main text.
Line 9: southern should not be with capital letter, please modify throughout the whole manuscript (line 20, 35, etc).
AUTHOR: Thank you for the helpful suggestion. We have implemented the necessary adjustments throughout the text.
Line 15: I read this now in the abstract but it is likely in the manuscript also. It is important when mentioning how human activity impacts brown hyena occupancy and detection probability to specify to the reader the little human activity present in your study area and also the level of persecution of the species, both when describing the study area and also in the discussion, so readers can compare your results (and the degree of human activity and disturbances) to other study sites and make your study more relevant.
AUTHOR: Thank you for this valuable comment. We clarified the low level of human disturbance within the CNP in the Discussion section, particularly in relation to the non-significant effect of anthropogenic covariates on brown hyena occupancy and detection probability. We also appreciate your suggestion to include this information in the Study Area section. In response, we have added a statement to make it clear from the outset that human presence in the CNP is minimal and exerts low impact on wildlife.
Line 17: Do hyenas prey in your study area or mainly scavenge? If you mention predatory behavior you should provide evidence of it, otherwise hyenas mostly scavenge and kleptoparasite with only usual predation recorded at seal colonies.
AUTHOR: Thank you for your thoughtful comment. We did not observe any direct evidence of brown hyenas engaging in hunting behaviour within the CNP. In response, we have removed the phrase “and a more predatory behaviour” from the sentence and revised the text to adopt a more cautious tone when referring to potential predatory behaviour, in line with the absence of direct evidence.
Line 21: In the southern Namib together with brown hyenas there are cheetahs, leopards and spotted hyenas (these ones occurring less than 150km from your study area but surely some individuals have been seen around). The only species missing are the lions and perhaps in some parts also spotted hyenas, if you mean these, please precise.
AUTHOR: Thank you for your comment. We acknowledge that the original wording may have been misleading, and we have revised the phrase to indicate a more limited applicability—specifically to arid environments where large predators such as lions and spotted hyenas are absent. In our two years of camera-trapping efforts, we recorded only a single detection of a spotted hyena, which occurred after the study period. Since then, the species has not been recorded again for over a year. For this reason, we refer to their status in the area as absent as there are only occasional sightings. Nonetheless, we remain hopeful about a potential future expansion of the species within the CNP.
Significance: 22-28: Please add the information available for brown hyenas in other study sites (coastal deserts, Kalahari). Even if data is not available on occupancy, there is quite some information on activity patterns and thus it can be mentioned that in your study area hyenas live in a desert without lions and away from coastal weather with stable food availability (e.g. seals).
AUTHOR: Thank you for your helpful suggestion. We have clarified that the findings from this study are particularly applicable to inland desert ecosystems characterized by scarce food availability, in order to distinguish them from ecologically different regions such as the Kalahari and coastal deserts. Given the strict 100-word limit, we have aimed to convey all information as clearly and concisely as possible.
Lines 36 and 37. This statement is not correct and the reference does not belong to any data provided on this. Namibia has stable and widely distributed numbers of members of the Hyanidae family. Their numbers have even increased over the last decade. Please read the Red data book published for carnivores in Namibia. It is available free online.
AUTHOR: Thank you for pointing this out. We acknowledge that using the present tense was inaccurate, as our intention was to refer to historical trends rather than current data. We have revised the sentence accordingly to reflect this historical context. The referenced source indicates that South Africa, Namibia, Angola, and Sudan experienced the greatest historical proportional loss in Hyaenidae species.
Line 41: modify for 4,365 – 10,111 and split the long sentence in two.
AUTHOR: Thank you for your suggestion. We have revised the sentence by splitting it into two for improved

readability. However, in accordance with the journal's guidelines, we are unable to use commas as thousand separators. Instead, we have followed the requirement to use spaces, and only for numbers greater than 10,000. We agree that this formatting may appear unusual, but we have adhered to the specified style.
Line 45: deemed stable. Yes that is correct thus you contradict what was written in line 36, see my comment about it (or clarify if I misunderstood).
AUTHOR: Thank you for your observation. We have revised the previously mentioned sentence accordingly to address your comment and improve clarity.
Line 47: remove strictly as I mentioned before.
AUTHOR: We proceeded with the suggested correction. Also, we decided to implement the Methods for the classification of the species as cathemeral, diurnal, nocturnal, and crepuscular following the recent paper published by Gerber et al. (2024) that allows for standardisation of diel phenotypes classification. By refining our methodology for calculating with much more precision sunset, sunrise, start of the night, and end of the night values, as well as crepuscular hours (twilight), we now present a highly precise classification. Accordingly, the brown hyena is now categorised as 'cathemeral', with 22.6% and 64.5% of detections at daytime and nighttime, respectively. We corrected both the Methods, the Results, and the Discussion sections to take into account these changes.
Line 48. What is being overlooked. Is there any word missing? Their?
AUTHOR: Thank you for highlighting this issue. Indeed, the phrase was not correct. We replaced "their" with "the species"
Line 51: This is not correct as I mentioned before. There is recent literature in this last decade (but I do agree that could be better).
AUTHOR: In alignment with the revisions made to the abstract, we have removed the sentence to avoid any potential misinterpretation and to ensure consistency throughout the manuscript.
Lines 53 and 54: Please do a basic search in researchgate. Just search for brown hyena. You will find many papers published within the las decade.
AUTHOR: Thank you for bringing this to our attention. It was not our intention to undervalue recent studies. Our statement was intended to refer specifically to recent spatial ecology research, particularly on occupancy. However, we acknowledge that the wording could be misinterpreted as suggesting a lack of recent publications on the species, which is not the case—as evidenced by the numerous studies we have cited. We have changed the phrasing to reflect this point.
Lines 55-56: please provide reference/s
AUTHOR: Thank you for your suggestion. We have added the appropriate references to support the relevant points and strengthen the manuscript.
Line 58: mention also kleptoparasitism
AUTHOR: Thank you for your suggestion. We have also included a reference to the species' kleptoparasite behaviour to provide a more comprehensive overview of its ecological strategies.
Lines 63-64 northern and central should not be capitalised
AUTHOR: Thank you for the helpful suggestion. We have implemented the necessary adjustments throughout the text.
Line 65 change the second "its" for "their"
AUTHOR: We proceeded to make the suggested change
Lines 68-69: This is inaccurate: Please modify the reference for number 3 (red data book of Namibia) which is more updated than 4 (IUCN Red List) and you will see in the distribution map that it is not correct. Easternmost should not be capitalised. Also not east (line 71)
AUTHOR: We clarified this with the suggested citation. We did not state clearly our point that was to underline that the area is close to the "zero presence" area for the national distribution range accounting for both the global and national assessment. We hope that with the new phrases we made it clear and accounted for the proper citations.
Line 71: I am unsure that they will disperse much into the east, but let's hope!
AUTHOR: Yes, we are very optimistic.
Line 76, remove the plural to other co-occurring predators if you only did it for the leopard. You also have cheetahs, caracals and black-backed jackals there. Why not also including Oryx, kudu and cheetahs? I am

not suggesting you should do it, just curious why it did not happen. Not enough data? Then it must be explained otherwise your study lacks of interactions from hyenas with key species.

AUTHOR: Thank you. We have removed the plural. We also included a more detailed explanation on covariate selection in the material and methods section.

The main reason for including only leopards in our analysis of predator interactions is that interference competition, particularly within predator guilds, is most likely to occur among carnivores of comparable body size, as noted in previous literature. Consequently, we excluded mesopredators such as *Black-backed jackals* from our analysis, as their ecological interactions with brown hyenas are likely to be limited or asymmetrical. Additionally, for caracals we only had 9 detections.

That said, we fully agree that exploring the temporal ecology of brown hyenas in sympatry with cheetahs would be of great interest. However, the extremely low number of cheetah detections in our dataset (n = 3), as well as similarly low detection rates for several other species listed in Supplementary Table 2, prevented us from conducting meaningful analyses for these taxa. In some cases, such as the cheetah, the very low RAI (0.06) may reflect a low local density and, consequently, limited temporal or spatial overlap with other carnivores, including the brown hyena.

We acknowledge the importance of these potential interactions and suggest that further studies - some of which are already underway - should specifically target these low-density species to better understand their temporal and ecological dynamics in this landscape.

As for prey species, we included springboks because they are the most abundant species in the study area and opportunistic predators are known to utilise most abundant prey species. Also, it could be the most abundant species for available remains to scavenge. We included Leporidae as it has been reported that brown hyenas hunt prey species of similar size.

Our selection of covariates was intentionally limited to a few key species—leopard, springbok, and Leporidae—to reduce the risk of overfitting, given the relatively low number of brown hyena detections. These species were chosen to reflect different ecological interactions: potential scavenging (springbok), hunting (hares and possibly springbok), and competition (leopard). We acknowledge that including a broader range of species could provide a more comprehensive understanding of the ecological dynamics in the area. Future and ongoing work aims to address this by incorporating a broader analytical framework, including multi-season and multi-year data.

Line 83: I would be very surprised if brown hyenas hunt (regularly) in your study area and it would definitely worth publishing that. If you do not have evidence of it, you should rather write kleptoparasite instead of hunting.

AUTHOR: Thank you for your insightful suggestion. As this section serves to introduce the study and outline the hypotheses, we have revised the text to mention only scavenging and kleptoparasitism. This avoids making any a priori assumptions about other behavioural strategies and ensures that the introduction remains appropriately focused and neutral.

Lines 84-87: Without yet reading the discussion, please ensure you mention the impact of high daily temperatures on wildlife and their activity patterns.

AUTHOR: Thank you for your comment. We addressed the limitation of considering only the dry season in the Discussion, acknowledging that this excludes potential seasonal and temperature-related influences on the species' temporal activity. Due to the strict word limit, we chose not to elaborate on the effects of temperature on activity patterns for all specie, and instead focused the discussion on the primary findings, such as activity overlap and occupancy results. We did explain the cathemeral behaviour registered for brown hyenas as a response to lower daily temperatures in the discussion.

Line 99: South West should not be capitalised as well in the line 100 and 101.

AUTHOR: Thank you for the helpful suggestion. We have implemented the necessary adjustments throughout the text.

Line 107: Add Atlas of Namibia (freely available online) as a reference

AUTHOR: Thank you for the suggested citation. We are familiar with the *Atlas of Namibia* and acknowledge its relevance. However, due to the strict reference limit of 60, we had to make careful and selective choices to remain within the allowed number. As the methodology section alone accounts for nearly half of the references, this significantly constrained our ability to include additional sources, despite their value.
Line 110, northern also not capitalised
AUTHOR: Thank you for the helpful suggestion. We have implemented the necessary adjustments throughout the text.
Line 112, you might also add elephants and rhinos (although they are in neighbouring reserves)
AUTHOR: Thank you for your insightful observation. We agree that this clarification would be valuable as both species are key ecological players. However, as the paragraph in question specifically focuses on the carnivore community, we have revised the text to refer explicitly to predators, thereby intentionally excluding herbivorous species to maintain thematic consistency.
Line 119: you can also add slender mongoose
AUTHOR: Thank you for the suggested addition. In our study, we aimed to include only species that were directly recorded within the study area of the CNP, and to date, we have not recorded the presence of the slender mongoose. To clarify that our reference pertains specifically to the local context, we have added the phrase “carnivore guild of CNP” to indicate that we are referring exclusively to species documented within this area.
Line 137 change was for were
AUTHOR: Thank you for noticing the error. We proceeded to fix it as suggested.
Line 150: is there a specific reason to choose 5 days over other different period (3 or 4 days)? Do you know how would this have affected your results?
AUTHOR: Thank you for your comment. We selected one of the sampling occasion discretisation periods recommended in the literature, guided by a preliminary assessment of our data. Specifically, we constructed detection matrices using 1-, 3-, 4-, and 5-day intervals. We ultimately chose a 5-day discretisation period, as the overall number of brown hyena detections was relatively low, and the shorter intervals resulted in matrices with a disproportionately high number of zeros (non-detections). Since an excess of zeros can cause convergence issues in occupancy models, we opted for the 5-day interval to ensure model stability and robustness. Additionally, it has successfully been used in similar occupancy works.
Line 174: why choosing Leporidae over Oryx and Kudu? You are more likely to find hyenas scavenging on Oryx and Kudu predated by cheetah and leopard than on hares. The likelihood of hyenas living/hunting on hares is very reduced in this ecosystem, (in comparison to the Kalahari or other ecosystems with higher grassland biomass). I believe that if you look at the abundance of these species in your camera traps, the ungulates will also be more abundant (and have a much higher biomass). This is something that should be explained with detail in your discussion to justify the choice of species.
AUTHOR: Thank you for your thoughtful comment. The selection of biological covariates was guided by two main criteria: 1. The need to limit the number of covariates to ensure model convergence. Given the relatively low number of brown hyena detections, including too many covariates led to model fitting issues. Although additional species were initially considered, the occupancy model could successfully run only with three covariates. 2. The selection of species was based on ecological relevance: leopard was included as a potential competitor or facilitator, springbok as the most abundant species in the study area and likely the primary food source in terms of biomass, and Leporidae to represent possible prey for predatory behaviour, as they have been reported in the species' diet. We agree that including a broader range of species would provide a more comprehensive understanding of the ecological dynamics. However, we had to work within the limitations of our dataset while still aiming to represent a range of potential interactions. We have revised the manuscript to better reflect these constraints and have added a more detailed explanation of the covariate selection process.
Line 226: remove capital letter to southern
AUTHOR: Thank you for the helpful suggestion. We have implemented the necessary adjustments throughout the text.

Line 248: remove 'the' before brown
AUTHOR: We proceeded to make the suggested change.
Line 249: Springbok without capital letter
AUTHOR: Thank you for noticing the error. We proceeded to fix it as suggested.
Line 256: It is striking mentioning potential prey and no providing info on Oryx, Kudu and Zebra.
AUTHOR: Thank you for your observation. We acknowledge that species such as oryx, kudu, and zebra are relevant in the context of potential prey. However, the selection of covariates for our analysis was constrained by both methodological and analytical limitations. We fully agree that including larger ungulates such as oryx, kudu, and zebra would contribute to a more comprehensive understanding of prey availability and ecological dynamics. However, due to the constraints mentioned, we were unable to incorporate additional covariates in this initial analysis. We have acknowledged this limitation in the manuscript and highlighted the need for future studies—including those using larger datasets or multi-season data—to incorporate a broader suite of prey species.
Lines 265 and 266: When mentioning human and vehicles, what type of activities were carrying the humans (tourists hiking, management park staff, researchers, others?), as well as vehicles? Please add info on this before the discussion.
AUTHOR: Thank you for your comment. We have incorporated this clarification into the "Data Analysis" section to provide a clearer explanation regarding the type of activities in CNP.
Line 269 southern without capital letter S
AUTHOR: Thank you for the helpful suggestion. We have implemented the necessary adjustments throughout the text.
Line 277: please add reference for arid environments (cite Ingrid Wiesel, red data book of Namibia (Hanssen et al.) or in the Kalahari from Gus Mills
AUTHOR: Thank you for your suggestion. We have added the reference to the *Conservation Status and Red List of the Terrestrial Carnivores of Namibia* to support and contextualize our discussion on species status and conservation relevance.
Lines 280 to 288: Does elevation really affect brown hyenas? or is it rather where vegetation is found, thus prey, thus other carnivores (leopard and cheetahs) and therefore scavenging opportunities? I would like to see something like that discussed here. I miss some basic and valuable biological and field knowledge discussing here the results. E.g. Hyenas use mountains to den but also to spend the day and rest because they are protected from the competitors and humans. At night, they roam in the more vegetated areas and frequented by game when searching for scavenging opportunities. Where you find springbok, oryx, zebra, you will find hyenas at night, foraging. You could identify where you detect hyenas at which time to understand their movement patterns and therefore explain when they are detected at certain locations. Detection probability is also influenced by where and how you deploy the camera traps and in some areas (riverbeds, valleys, mountain ridges), it is difficult to cover the landscape enough with camera traps to ensure every hyena will be photographed and some landscapes are more difficult to cover. Therefore, the landscape also plays a role, not only brown hyena ranging behaviou**r**. It would be good to mention the targeted locations to deploy the camera traps. All of this may seem obvious but worth to discuss (or at least part of it).
AUTHOR: Thank you for your comment. We used elevation as a proxy to represent the clear topographical distinction between the plateau and the canyon within the study area. While elevation did show a positive influence on brown hyena occupancy, we acknowledge that it also reflects a broader set of ecological differences between these two zones. As noted in the manuscript, our findings suggest that brown hyenas appear to use the plateau more extensively than the lower canyon during the dry season, likely due to the higher densities of ungulates in that area. Indeed, most detections occurred at camera trap stations situated along the plateau's edge—particularly near secondary canyons—though not exclusively. We have aimed to capture these nuances in the text to clarify the ecological interpretation of elevation in our analysis.
Line 290 southern without capital letter
AUTHOR: Thank you for the helpful suggestion. We have implemented the necessary adjustments throughout the text.

Lines 291 to 296: well, I see here some of the thoughts I discussed in the paragraph above 😉
AUTHOR: Thank you for your kind feedback. We are pleased that the interpretation provides a more comprehensive perspective and is appreciated. Your comments have been valuable in helping us improve the clarity and depth of the manuscript.
Line 297: sorry but I still stumble that there is no reference yet to other species such as cheetah, oryx, kudu and zebra.
AUTHOR: Thank you for your comment. In response, we have included a more detailed explanation of our covariate selection process to clarify the rationale behind the exclusion of other species. This addition aims to address the concern regarding the lack of reference to certain species and to better reflect the analytical and methodological considerations that guided our choices.
Lines 307-308: Do you have any evidence of brown hyenas predating on leporids in your study area? As well as what part of their diet they contribute to? Are these thoughts mostly driven by other ecosystems such as the Kalahari where leporids have a much higher density? You surely have camera trap pictures of hyenas carrying food back to their dens, what prey items can you see? When you mention the likelihood of predator encounters, do you mean leopards and cheetahs or hyenas themselves? Please clarify. Do you have data on springbok density in comparison to other species of ungulates? If so, this data could back up why you choose such species.
AUTHOR: Thank you for your thoughtful and constructive comment. We do not currently have direct evidence of predation on hares in the study area, nor do we have data on diet composition, as scat analyses have not yet been conducted. Photographic evidence of brown hyenas carrying food is limited, and in the few instances where such behaviour was observed, the prey remains appeared to be ungulate limbs. In revising the manuscript, we have taken care to interpret the results more cautiously. We also identified and corrected an error in the interpretation of the Leporidae covariate: its effect on brown hyena detection probability was, in fact, negative—not positive as previously stated. Given the ambiguous nature of this relationship, we have avoided overinterpreting the result. Regarding springbok, we have clarified in the text that this species is known to be predated by other carnivores. Its inclusion as a covariate was based on its high relative abundance in the study area (as shown in Supplementary Table 2), making it a likely food source through both scavenging and potential opportunistic predation. We also highlight the importance of future studies incorporating additional predator and prey species to better understand these ecological interactions. The rationale for covariate selection has been more clearly explained in the revised manuscript.
Line 327. The references are wrong. Number 54 matches with a cougar study not with brown hyena. I did not check the other references but the issue may be also found throughout the text if a reference/number shifted. Check it out. It would be good to add some references from hyenas in other southern African ecosystems (Kalahari, coastal Namibia).
AUTHOR: Thank you for noticing this oversight. We have carefully revised all references and numerical details to correct the error and ensure consistency throughout the manuscript. We fully agree that including additional references would enhance the contextual depth of the work. In earlier drafts, we did include a broader range of sources; however, the strict limit of 60 references required us to make difficult decisions and omit several valuable citations. We prioritized those most directly relevant to our objectives, while striving to maintain a balanced and well-supported discussion
Line 335. The low RAI values of cheetahs and leopard depend highly on where you set the camera traps. They indeed must live a low densities but likely higher than your camera traps recorded, otherwise check for recaptures of territorial individuals, if you see few, this is indication that you struggle to capture them (which is normal in such landscape!). I would be careful with such statement. Brown hyenas do not hunt (usually) in the Namib desert and I know this via GPS movement data of hyenas, cheetahs, leopards and lions. Hyenas move more than cheetahs and leopards and this is the reason you may capture them more than these cats.
AUTHOR: Thank you for your detailed comment. Regarding cheetahs, we recorded very few detections during the study period—only three captures—and identified fewer than six mature individuals based on preliminary photo-identification. These results suggest a very low density of cheetahs in the study area. While we acknowledge the limitations of camera trapping as a method and the possibility that actual densities may be higher, we believe our interpretation is justified given the available data.

As for leopards, their detection frequency and Relative Abundance Index (RAI) values were slightly lower than those of brown hyenas throughout the study period. Preliminary identification of individuals also suggests low density (specific values can be added if available). Based on our data, leopard and brown hyena abundances appear comparable and consistently low. Moreover, only about 50% of sites where brown hyenas were detected also recorded leopards, indicating a partial overlap in spatial distribution. We are mindful of the limitations associated with camera-trapping methods, particularly the risk of underdetection. To mitigate this, we designed our sampling strategy to maximize detection probabilities by maintaining a minimum spacing of 2 km between camera traps and selecting optimal field locations such as latrines, scent-marking areas, game trails, road intersections, waterholes, natural springs, and canyon bottoms. It is important to note that this study represents a preliminary investigation into the spatial ecology of these species and is based on data collected over a single season. We have revised the manuscript to better acknowledge these limitations and frame our findings accordingly.
Line 338: What is the sample size you have to support this statement?
AUTHOR: The temporal activity of the leopard has been derived from 28 observations, the brown hyenas from 31.
Line 340: Hyenas would chase off big leopard males and a coalition of cheetahs from their carcass and rarely would wait for them to finish off their meal.
AUTHOR: Thank you for your thoughtful observation. We acknowledge that brown hyenas are indeed capable of displacing other predators from kills. The intention behind the original sentence was to highlight a general tendency among scavengers to show peak activity following that of primary predators—either to opportunistically locate fresh kills or to potentially displace other species. It was not intended as a definitive statement on behavioural strategy. We recognise that the term "leftovers" may not adequately reflect the full range of behavioural tactics employed by brown hyenas. Additionally, given the large spatial scale of the study area and the low densities of large predators, direct interactions between species are likely infrequent. This suggests that many scavenging events may occur at unattended carcasses; however, we acknowledge this is based on observational inference rather than direct evidence. To address this and avoid implying a passive "sit-and-wait" strategy, we have reworded the relevant sentence to more accurately reflect the flexible and opportunistic nature of brown hyena scavenging behaviour.
Lines 341-344. Edwards et al. had a low sample size (which is common in the desert) and the other studies you compare to are in more mesic areas with much larger sample sizes. I would be careful to take such conclusions (that hyenas do not scavenge in your study area as much because of your findings on activity patterns).
AUTHOR: Thank you for your thoughtful feedback. We apologise if the intended interpretation of our temporal analysis was not clearly conveyed. Our conclusion—that brown hyenas may exhibit a degree of independence from leopards in this context—was based on a combination of observations: the moderate temporal overlap (approximately 60%, which is notably lower than reported in other studies) and the lack of a significant effect of leopard presence on brown hyena habitat use. We acknowledge that this does not constitute evidence of predation by brown hyenas. However, given their broad and flexible diet, it is plausible that they access alternative food sources, including carcasses resulting from natural mortality—resources that leopards may also utilise. In light of the low abundance of both species in the study area, our aim was to highlight the ecological adaptability of brown hyenas and to encourage a nuanced interpretation of their relationship with leopards. In particular, we suggest that in certain environments, competition and resource availability may play a more prominent role than facilitative interactions in shaping their ecological dynamics. We have revised the manuscript to better reflect this interpretation and ensure clarity.

Lines 348: I think that by not adding cheetahs, oryx, kudu and zebra, you are missing part of the picture. Cheetahs are more diurnal than leopards, cheetahs leave more food behind and are easier to drive away from their kills than leopards. The activity pattern you may see from the hyenas may be an overlap with both cheetahs and leopards to increase scavenging opportunities. I would like to see something like this in the discussion which would also mention the limitation of this study.

AUTHOR: Thank you for your valuable comment. We agree that including a broader range of species would provide a more comprehensive analysis. However, due to the very low number of cheetah detections during the study period, it was not feasible to include this species in the analysis. We acknowledge that this low detection rate could reflect either a genuinely low population density or limitations in our ability to detect the species through the chosen sampling design.

Our methodology was tailored specifically to target large and medium-sized carnivores, and we believe it was appropriate for capturing the activity of such species. While some underestimation is inevitable, we are confident that our data reflects a genuinely low abundance of cheetahs in the study area. As such, we consider our conclusions regarding interactions with other predators to remain valid.

Regarding prey species, we opted not to include larger-bodied species for reasons outlined in earlier responses, primarily to avoid overfitting the model given the limited number of detections for our target species.

In response to your comment, we have expanded the discussion to more clearly acknowledge these limitations, ensuring readers are aware of the potential constraints and avoiding possible misinterpretation.

Lines 355 to 357. I repeat what I wrote above. The lack of data from other species here drives to such conclusions because you can't see the whole picture (missing activity patterns of other interacting species such as cheetahs and more ungulates), in my point of view incorrect. If you have data to back-up that hyenas hunt in your study area, you should present it but no study in Namibia reported hyenas hunting away from the seal colonies (also no observations to my knowledge from the whole research field community).

AUTHOR: Thank you for your comment. As mentioned in previous responses, we have provided a detailed rationale for our covariate selection and have revised the manuscript to present a more moderate and cautious interpretation of the results.

The suggestion of possible hunting behaviour by brown hyenas was based on two main considerations: first, the absence of a significant effect of leopard abundance on brown hyena occupancy, coupled with a relatively lower temporal overlap; and second, a desire not to entirely exclude the possibility of predatory behaviour, especially given the species' known ecological flexibility.

To reflect the speculative nature of this interpretation, we have used conditional language and have also introduced an alternative explanation—namely, that brown hyenas may rely on carcasses resulting from natural mortality rather than active hunting. These revisions aim to ensure a balanced and scientifically sound interpretation of the findings.

Lines 369-371: Which larger predators are being proposed to be reintroduced in the area? Do you have more information on this, then please develop.

AUTHOR: The primary consideration has been the potential reintroduction of spotted hyenas, although there have also been discussions regarding lions. However, the reintroduction of lions is unlikely to be approved at this stage.

Line 386. Table one. The information and the justification of the species is well displayed and comprehensive. I must say that in such complex ecosystem with multispecies occurring at low densities but highly competing for resources, to have a good understanding that enables you to interpret your results, you need to include more species within your analyses or mention such limitation in your study (already limited by the characteristic low sample sizes of arid environments) and a more careful interpretation of the results.

AUTHOR: Thank you for your thoughtful comment. We agree that capturing the full range of ecological interactions influencing brown hyena presence and activity is challenging, particularly given the limited sample size. As noted in our responses above, we have revised the text to adopt a more cautious interpretation of the results and to clearly acknowledge the limitations of the study.
Line 411, figure 3. This is likely the more diurnal activity pattern I ever observed from leopards which is very surprising due to the high daily temperatures. Do you have any explanations for this? How many pictures/events support this? From May to October it covers the coldest months of the year, thus it may explain that leopards were more diurnal than expected. If the camera trap survey is done during the hottest months, I could potentially affect your results. I think this should be mentioned in your discussion.
AUTHOR: Thank you for your insightful comment. The number of leopard detection events recorded during the study period was 28. Within the CNP during the dry season, temperatures—particularly on the plateau—remain low throughout much of the morning and tend to rise only during the central hours of the day. Additionally, the area is characterized by frequent cold winds and fog, which further contribute to lower temperatures. Thus, as you mention, temperature most likely influenced leopard activity. We chose not to expand on this aspect in the Discussion, as a detailed commentary on the activity patterns of individual non-target species would have shifted the focus away from our primary research objective centred on brown hyenas. However, we fully acknowledge the relevance of this observation and intend to explore leopard activity patterns more thoroughly in future work.
References: double check that your reference**s** match with the numbers in the text.
AUTHOR: Thank you for your comment. We have carefully revised all references and numerical details to correct the error and ensure consistency throughout the manuscript.
Supplementary table 2: This table answers many of my questions. It is obvious that with only 3 cheetah detections, the species can't be included in the analyses. Please mention this in the text.
AUTHOR: Thank you. We have addressed this in the manuscript.

Reviewer 3: Round 1
Date completed: 08 April 2025
Conflicts of interest: None

Recommendation: Accept / Revisions required / Resubmit for review / Resubmit elsewhere / Decline / See comments
REVIEWER: Revisions required
With regard to our policy on 'Publishing peer review reports', do you give us permission to publish your anonymised peer review report alongside the authors' response, as a supplementary file to the published article? Publication is voluntary and only with permission from both yourself and the author. Yes/No
REVIEWER: Yes
Comments to the Author: This study explores space use (occupancy and detection) and diurnal activity of brown hyenas in the Fish River system in southern Namibia in relation to topographic, biotic (prey and other predators) and anthropogenic variables. The authors restrict inference to this system, which I think is good. I had some questions about the way model selection was carried out but it looks like the variables considered mostly affected detection probability. The activity analysis showed a clear nocturnal activity peak. Specific comments: Line 40: what is an "estimated minimum range"? Is this some kind of confidence interval? For the estimated population size? Clarify. Lines 59 to 72: this is not a clear description of the research gap. It doesn't do you much good to claim that earlier studies are controversial without explaining why. Point (ii) is entirely unclear to me. I recommend just saying what the research gap is (perhaps point (iii), i.e. spatial ecology is understudied?). What I gather from all these lines of text is that the research gap is the activity patterns of brown hyenas in southern inland Namibia?

Line 67: “spatio–temporal behaviour” sounds a bit vague to me as behaviour could relate to many things. Perhaps “spatio–temporal activity” would be better?

Line 82: “ relative abundance of prey species” relative to what?

Line 145 and the equation in line 144: “ith covariates” should that be “ith site”, rather? And I think “n detection” and “sampling effort” should then also be indexed by i, i.e. they vary across sites, right?

Line 168 to 172: spell out TPI, TRI and TWI on first use. “TPI calculated as the difference…” in what?

Line 187: what models do you call saturated?

Line 198: “20 independent observations” is this pooling across sites, or a specific site?

Lines 225 – 227: I’m not sure I understand all these numbers. I understand that you had 42 stations that were active for 129.1 on average, which yields 5422 trapping days. But how do you get to the potential effort of 5556? And what exactly is does the 112.47 in line 225 refer to? Make this clearer. Also, for the occupancy analysis, you said you pooled data into 5-day periods (line 151) and so the most relevant information would be the number of 5-day periods you used.

Line 232: “None of the variables showed collinearity issues (i.e., VIF ≥ 3) “ Do you mean smaller than 3? Large values are a problem.

I appreciate Table 1 where you give the rationale of why you considered each variable and the expected direction of effect. For elevation, could you give a bit more information on the conflicting hypotheses? And what was the reason for including TPI and TRI?

Lines 233 to 253 and tables 2 and 3: I appreciate you structuring your models into groups with environmental, biological and anthropogenic variables. I think this is a great approach. However, I find it misleading to then analyse these groups of models independently. The models with environmental covariates on detection are clearly better than any of the other groups. Delta AIC should be calculated against the overall best model, not within groups. Also, you don’t need to repeat the constant model six times across the two tables.

Model selection: I understand that you kept either the detection or occupancy model constant when adding variables to the other model part. This is a bit dangerous. I appreciate your attempts at keeping the number of fitted models limited but the top of table 2 suggests that detection varies with environmental covariates. When you then set detection to constant and add these variables to the occupancy part, it is not surprising that they try to pick up some of this variability in the data and this doesn’t mean that occupancy is in fact explained by these variables. There are several model selection strategies for such multi-component models and there is no consensus about what the best strategy is (see Doherty et al 2012, J Ornithol 152 (Suppl 2):S317–S323). But you need to make sure that the detection model adequately describes variation in detection probability before you can conclude that the same variables also explain variation in occupancy, and vice versa. One common strategy is to first find the best detection model. Then keeping this detection model, one explores different occupancy models. And finally, with the best occupancy structure, one can explore dropping variables from the detection model again. I would then present the entire model selection analysis in a single table, perhaps with subdivisions. It will be a large and unwieldy table, I know, but it will be easier to show what the overall best model is. And the interpretation would then be easier to follow.

This will also affect your results section. All those ‘best’ models with ‘non-significant’ covariates will no longer be the best models when compared across all fitted models.

I'm curious why sampling effort had a negative effect on detection probability.

I understand you used step-wise model selection on the subsets of models. In the absence of a more specific a-priori model set, this is fine. But it makes your analysis more exploratory in nature. Make sure you interpret the results in that light. Also, somewhere you need to state how many models you fitted in total.

Table 4: Cumulative model weights only make sense if you have a balanced candidate model set, i.e. if all covariates appear in the same number of models. I think you fitted all possible combinations of covariates, in which case this would be true. Explain your model selection more clearly.

Lines 280 to 298: here you are interpreting the correlation between variables and detection probability as giving us insight into the species spatial ecology. I don't quite follow that. I would have thought this just means that the species is easier to detect in certain places compared to others, given that it occurs there.

Line 334: "can only kleptoparasite leopards" should be "can only kleptoparasitise leopards"?

Author response to Reviewer 3: Round 1

Line 40: what is an "estimated minimum range"? Is this some kind of confidence interval? For the estimated population size? Clarify.

AUTHOR: Thank you for your insightful comment. We have removed the term "minimum range" as we recognize that it may have caused confusion. The phrase was originally intended to convey a conservative global population estimate, derived by summing the lowest values from country-specific assessments. While this approach likely underestimates the true number—acknowledged by the IUCN Red List as well—it is not essential to the main objectives of this study. Given the manuscript's strict word limit, we chose to prioritize more critical content and have omitted this phrase accordingly.

Lines 59 to 72: this is not a clear description of the research gap. It doesn't do you much good to claim that earlier studies are controversial without explaining why. Point (ii) is entirely unclear to me. I recommend just saying what the research gap is (perhaps point (iii), i.e. spatial ecology is understudied?). What I gather from all these lines of text is that the research gap is the activity patterns of brown hyenas in southern inland Namibia?

AUTHOR: Thank you for your helpful feedback. We have revised the sentence to more clearly articulate the research gap. As you suggested, we removed point 1, as addressing the controversial findings in detail would require substantial discussion better suited for another context. These contrasting results are now briefly referenced in the Materials and Methods section to support the rationale behind our covariate selection.

Point 2 has been reworded to emphasize that previous studies were conducted in areas with ecological conditions distinct from those of the CNP—particularly in terms of carnivore guild composition—which may influence species interactions and behavioural patterns. This clarification helps to better frame the relevance and uniqueness of our study context.

Line 67: "spatio–temporal behaviour" sounds a bit vague to me as behaviour could relate to many things. Perhaps "spatio–temporal activity" would be better?

AUTHOR: Thank you for your suggestion. We agree with your observation and have revised the text accordingly by replacing "behaviour" with "activity".

Line 82: " relative abundance of prey species" relative to what?

AUTHOR: Thank you for your comment. The term "relative" was used to indicate that our estimates are based on a Relative Abundance Index (RAI), rather than absolute density values. Due to data limitations, we were not able to obtain accurate density estimates and thus relied on RAI as a proxy measure to assess species presence and activity levels across the study area.

Line 145 and the equation in line 144: "ith covariates" should that be "ith site", rather? And I think "n detection" and "sampling effort" should then also be indexed by i, i.e. they vary across sites, right?

AUTHOR: Thank you for pointing this out. The term “ith covariates” was a typographical error and should have read “ith species.” Regarding the indexing of “n detections” and “sampling effort,” we intentionally did not include specific indices in the formula, as the Relative Abundance Index (RAI) was calculated both across all sites—to provide an overall estimation for each species (see Supplementary Table 2)—and per site, to derive covariates for the analysis. Our aim was to present a general formula applicable to both scales of calculation. We included an explanation in the text to avoid confusion.
Line 168 to 172: spell out TPI, TRI and TWI on first use. “TPI calculated as the difference…” in what?
AUTHOR: Thank you for your comment. As TPI, TRI, and TWI were already spelled out in the Introduction, we chose not to repeat the full terms in the Materials and Methods section to avoid redundancy. However, we agree that the meaning of the TPI calculation required clarification, and we have added “in elevation” to specify the nature of the difference being measured.
Line 187: what models do you call saturated?
AUTHOR: Thank you for your helpful suggestion. We agree that the term “saturated” may have been unclear to some readers. To improve clarity, we have replaced it with “complex” to better convey that these were the most parameterized models. Additionally, we revised the following sentence to avoid repetition by referring to them as “these.”
Line 198: “20 independent observations” is this pooling across sites, or a specific site?
AUTHOR: It is intended across sites.
Lines 225 – 227: I’m not sure I understand all these numbers. I understand that you had 42 stations that were active for 129.1 on average, which yields 5422 trapping days. But how do you get to the potential effort of 5556? And what exactly is does the 112.47 in line 225 refer to? Make this clearer. Also, for the occupancy analysis, you said you pooled data into 5-day periods (line 151) and so the most relevant information would be the number of 5-day periods you used.
AUTHOR: Thank you for your thoughtful comment. The term “potential effort” refers to the total number of days camera traps were intended to be active in the field, including days lost to malfunctions or battery depletion. While the theoretical sampling effort was 5,556 trap-days, the actual effective effort was 5,422. We have clarified this distinction in the manuscript. The previously reported figure of 112.47 was derived from calculations that accounted for double cameras deployed at certain sites later in the study, which contributed to a shorter sampling duration. However, we recognize that this detail may be misleading and is not essential to the core analysis, particularly as each camera site is treated as a single unit regardless of the number of devices. We have therefore removed that sentence from the text. As suggested, we have also added the number of sampling occasions (5-day intervals) resulting from the temporal discretization used in the analysis.
Line 232: “None of the variables showed collinearity issues (i.e., VIF ≥ 3) “ Do you mean smaller than 3? Large values are a problem.
AUTHOR: Thank you for your comment. The phrase “i.e., VIF ≥ 3” was intended to define the threshold we used to identify potential collinearity issues. To improve clarity, we have revised the sentence to read “(i.e., none yielded a VIF ≥ 3),” making the criterion more explicit and easier to interpret.
I appreciate Table 1 where you give the rationale of why you considered each variable and the expected direction of effect. For elevation, could you give a bit more information on the conflicting hypotheses? And what was the reason for including TPI and TRI?
AUTHOR: Thank you for your helpful suggestion. As recommended, we have included additional details in the manuscript to clarify the rationale behind our covariate selection, aiming to enhance transparency in our methodological approach. With regard to TPI and TRI, to our knowledge, these indices have not previously been applied in studies of brown hyena occupancy, and therefore no specific references were available. However, we have specified that these variables were included because they effectively capture aspects of the complex topographical variation within the study area. We considered that small-scale topography could influence species’ spatial behaviour, and we sought to explore this potential relationship through the inclusion of these terrain variables.

Lines 233 to 253 and tables 2 and 3: I appreciate you structuring your models into groups with environmental, biological and anthropogenic variables. I think this is a great approach. However, I find it misleading to then analyse these groups of models independently. The models with environmental covariates on detection are clearly better than any of the other groups. Delta AIC should be calculated against the overall best model, not within groups. Also, you don't need to repeat the constant model six times across the two tables.

AUTHOR: Thank you for your constructive feedback and for appreciating our approach in structuring the models by covariate type. We understand your concern regarding the comparison of model performance within rather than across groups.

We chose to divide the models into three thematic groups—environmental, biological, and anthropogenic—due to limitations in model fit when attempting to include covariates from different categories in the same models. Specifically, preliminary analyses that incorporated a wider set of covariates across groups often resulted in convergence issues and a lack of model stability, likely due to the relatively low number of detections for the focal species. As a result, we opted to assess each group independently to preserve model reliability and interpretability.

This grouped structure also served an ecological purpose: it enabled us to isolate and better understand the relative influence of different types of variables (e.g., landscape features vs. species interactions vs. human disturbance) on brown hyena occupancy and detection. We believe this approach provides a more nuanced perspective on the species' spatial ecology, especially in a data-limited context.

That said, we fully acknowledge the limitation this introduces, particularly with regard to the comparability of model outputs across groups. We agree that, ideally, model selection and AIC comparisons should be made across all candidate models. To address this, we have revised the manuscript to clarify our reasoning and have emphasized that delta AIC values are interpreted within the context of grouped comparisons, rather than across the entire model set.

Additionally, we appreciate your point regarding the repetition of the constant model across tables. We have now streamlined the tables to remove redundancy and improve clarity.

We view this study as a preliminary step, and future research—with larger datasets and multi-seasonal coverage—may allow for the integration of a broader and more inclusive set of covariates into unified models. We have added a note in the Discussion to reflect this direction.

Model selection: I understand that you kept either the detection or occupancy model constant when adding variables to the other model part. This is a bit dangerous. I appreciate your attempts at keeping the number of fitted models limited but the top of table 2 suggests that detection varies with environmental covariates. When you then set detection to constant and add these variables to the occupancy part, it is not surprising that they try to pick up some of this variability in the data and this doesn't mean that occupancy is in fact explained by these variables. There are several model selection strategies for such multi-component models and there is no consensus about what the best strategy is (see Doherty et al 2012, J Ornithol 152 (Suppl 2):S317–S323). But you need to make sure that the detection model adequately describes variation in detection probability before you can conclude that the same variables also explain variation in occupancy, and vice versa. One common strategy is to first find the best detection model. Then keeping this detection model, one explores different occupancy models. And finally, with the best occupancy structure, one can explore dropping variables from the detection model again. I would then present the entire model selection analysis in a single table, perhaps with subdivisions. It will be a large and unwieldy table, I know, but it will be easier to show what the overall best model is. And the interpretation would then be easier to follow.

This will also affect your results section. All those 'best' models with 'non-significant' covariates will no longer be the best models when compared across all fitted models.

AUTHOR: Thank you for this thoughtful and detailed comment, as well as for pointing us to Doherty et al. (2012). We fully agree that in multi-component models like occupancy models, it is important to account for potential interactions between the detection and occupancy components, and that an inadequate detection model can compromise the interpretation of the occupancy results.

In principle, we support the recommended stepwise approach: identifying the best detection model first, then testing occupancy structures based on that detection formulation, and finally evaluating whether any detection variables can be removed. However, in practice, our dataset did not support this more complex modelling strategy.

Specifically, we found that using the full detection model—including the best-fitting detection structure (effort + Elevation + TPI)—in combination with multiple occupancy covariates resulted in poor model fit, as assessed by the *parboot* function for goodness-of-fit testing. Moreover, parameter estimates were highly unstable, with standard errors often exceeding the estimates themselves by a large margin. For example:

- Elevation: Estimate = 27.3, SE = 64.7
- TPI: Estimate = -102.2, SE = 251.9
- TWI: Estimate = 44.4, SE = 236.2
- TRI: Estimate = -40.1, SE = 147.2

This pattern held even in simpler model combinations and across the other groups of covariates (biological and anthropogenic). We attribute this to the low number of detections across sites, which limits the model's ability to support multiple parameters without overfitting.

For this reason, we adopted a strategy in which detection and occupancy covariates were tested within separate, structured model sets, keeping one component constant while varying the other. This allowed us to evaluate the influence of covariates within each group while maintaining model convergence and interpretability. We acknowledge that this limits direct comparison of models across the full covariate space and have now clarified this in the Methods section, along with the implications for interpreting the results.

We also appreciate your point regarding the structure of the model selection tables and the potential confusion caused by presenting "best" models within each group. In response, we have revised the relevant section of the manuscript to reflect a more cautious interpretation of these models, clearly indicating that comparisons were made within constrained subsets rather than across all models.

I'm curious why sampling effort had a negative effect on detection probability.

AUTHOR: Thank you for this interesting observation. We agree that the negative effect of sampling effort on detection probability was unexpected, as one would typically anticipate a neutral or positive relationship. However, we believe this result may be influenced by a combination of ecological and methodological factors specific to our study context.

First, the overall low density of brown hyenas in the study area, as indicated by the limited number of detections, likely plays a key role. In such conditions, increased sampling effort—particularly in areas where the species is absent or only transient—may simply accumulate more non-detections without improving the chance of encountering individuals. This could lead to a statistical artifact in which greater effort is correlated with lower detection probabilities.

Second, this result may also reflect the spatial distribution of effort. Sites with longer deployment times may coincide with areas of lower hyena activity, or where movement patterns are more sporadic, resulting in effort being expended in locations with minimal presence.

While this finding should be interpreted with caution, we believe it highlights the challenges of working with elusive species in arid, low-density landscapes, where more effort does not always equate to higher detection.

I understand you used step-wise model selection on the subsets of models. In the absence of a more specific a-priori model set, this is fine. But it makes your analysis more exploratory in nature. Make sure you interpret the results in that light. Also, somewhere you need to state how many models you fitted in total.

AUTHOR: Thank you for your thoughtful comment. We confirm that the model selection process was carried out manually in a step-wise manner, rather than through an automated algorithm. This approach enabled us to incorporate ecological reasoning into the selection of candidate models, rather than relying solely on statistical fit. In the absence of a well-defined a priori model set, we agree that this approach positions our analysis as exploratory in nature.

In recognition of this, we have taken care to interpret the results with caution, avoiding strong or overly deterministic conclusions. Throughout the manuscript, and particularly in the Discussion, we have framed our findings within the limitations of the study—namely, the single-season design, relatively low number of detections, and limited number of covariates included in the final models.

As suggested, we have also added a statement to the Methods section specifying the total number of models tested across the different covariate groups, to provide transparency and context for the reader.

We appreciate your guidance in highlighting the importance of aligning the interpretation of the results with the exploratory nature of the analysis, and have revised the manuscript accordingly to reflect this more clearly.

Table 4: Cumulative model weights only make sense if you have a balanced candidate model set, i.e. if all covariates appear in the same number of models. I think you fitted all possible combinations of covariates, in which case this would be true. Explain your model selection more clearly.

AUTHOR: Thank you for this important observation. You are absolutely right that cumulative model weights are only meaningful when derived from a balanced candidate model set—i.e., when all covariates appear in the same number of models. In the original version of the manuscript, we calculated these weights based on a stepwise, manual simplification process, which did not ensure a balanced model set and therefore may have led to biased cumulative weights.

In response to your comment, we revised our model selection procedure and re-fitted all possible combinations of the covariates within each model group to generate a fully balanced candidate model set. This allowed us to calculate cumulative weights correctly and consistently.

We have updated Table 4 accordingly and revised the corresponding section in the Results to reflect the recalculated values. We have also clarified our model selection approach in the Methods section to ensure transparency and reproducibility.

We appreciate your feedback, which helped us improve the rigour of this aspect of the analysis.

Lines 280 to 298: here you are interpreting the correlation between variables and detection probability as giving us insight into the species spatial ecology. I don’t quite follow that. I would have thought this just means that the species is easier to detect in certain places compared to others, given that it occurs there.

AUTHOR: Thank you for this important clarification. You are right—the detection probability model alone should not be used to draw conclusions about the species' spatial ecology, as it reflects the likelihood of detecting the species where it is present, rather than its actual spatial distribution or habitat preferences.

In our revised interpretation, we now combine insights provided by the detection and the occupancy models to interpret the species spatial ecology.

Line 334: “can only kleptoparasite leopards” should be “can only kleptoparasitise leopards”?

AUTHOR: Indeed, thank you for noticing it. We fixed it accordingly.

Reviewer 1: Round 2
Date completed: 22 June 2025
Conflicts of interest: None

Recommendation:
Accept / Revisions required / Resubmit for review / Resubmit elsewhere / Decline / See comments

REVIEWER: See comments

With regard to our policy on ‘Publishing peer review reports’, do you give us permission to publish your anonymised peer review report alongside the authors’ response, as a supplementary file to the published article? Publication is voluntary and only with permission from both yourself and the author.

Yes/No

REVIEWER: Yes

Comments to the Author:
I think that one word is missing in line 387.

Author response to Reviewer 1: Round 2

Thank you for your comment, we have corrected the phrase and added the missing word.

Reviewer 2: Round 2
Date completed: 26 June 2025
Conflicts of interest: None

Recommendation:
Accept / Revisions required / Resubmit for review / Resubmit elsewhere / Decline / See comments

REVIEWER: Accept

With regard to our policy on 'Publishing peer review reports', do you give us permission to publish your anonymised peer review report alongside the authors' response, as a supplementary file to the published article? Publication is voluntary and only with permission from both yourself and the author.
Yes/No

REVIEWER: Yes

Comments to the Author:
I am satisfied with the changes made and all comments and suggestions were tackled. I am happy with the latest version of the manuscript and I have no further comments. Good luck with the publication process and with your research career.

Author response to Reviewer 2: Round 2

We sincerely appreciate your positive feedback and the time and effort you dedicated to reviewing our work. We truly appreciate your thoughtful comments that have significantly improved the quality of our manuscript.

We are thankful for your kind wishes and support, and we look forward to the next steps in the publication process. Some changes have been made in light of other reviewers' comments. All changes were highlighted with 'track changes' throughout the main body text to enhance clarity.

We hope that, with these revisions, you will still find our manuscript suitable for publication in the South African Journal of Science.

Reviewer 3: Round 2
Date completed: 10 June 2025
Conflicts of interest: None

Recommendation:
Accept / Revisions required / Resubmit for review / Resubmit elsewhere / Decline / See comments

REVIEWER: Revisions required

With regard to our policy on 'Publishing peer review reports', do you give us permission to publish your anonymised peer review report alongside the authors' response, as a supplementary file to the published article? Publication is voluntary and only with permission from both yourself and the author.
Yes/No

REVIEWER: Yes

Comments to the Author:
The supplementary information seems to be missing from the revised ms.

I still find the model selection analysis somewhat misleading. The reference model keeps changing because you are only comparing models within subsets. For example in table 2, Model p(effort + Elevation + TPI + TWI + TRI), psi(.) is the worst supported model within the batch and yet is is a lot better supported than Model p(effort + Homo), psi(.), which is the best model in another batch. The same thing applies even between different tables: the best model in Table 3 is actually a lot worse than the entire group of models with environmental covariates in Table 2. You need to be quite a careful reader familiar with AIC-based model selection to notice this.

My interpretation is that we actually have very little evidence that occupancy is related to any of the covariates. Some of the models with covariates on occupancy are better than the null model, for sure, but they might just be picking up variation in detection that these models don't allow for and that we know are important from Table 2.

I understand the data limitations and that you can't look at models with covariates on detection and occupancy at the same time. But I feel the honest thing would be to say that the data are inconclusive about what causes variation in occupancy. At the very least, you need to guide the reader much more carefully.

Related to above, in line 205 " Akaike's weight (ωi), which represents the amount of variance described by the top–ranking model compared to all the other models" is not quite correct. It's only compared to models in the same subsection of the table. I think it would be better if it was indeed compared to all models.

And, line 206 "...covariate weights were calculated by summing Akaike weights across all models in which a covariate appeared". Here, I assume that you recalculated Akaike weights by treating all fitted models as a single set. Otherwise, the covariate weights would not make sense to me. But then I'm a bit surprised by the results since all models with covariates on occupancy (and constant detection) should have very small weights when properly compared across all models, so the weights can't sum up to very much.

Lines 256 to 265: this entire paragraph needs a big disclaimer that these effects are under the assumption of constant detection probabilities, i.e. ignoring the results of the paragraph immediately before this one.

I might be overlooking it but I can't find the information on how many models you fitted in total, which you said in your response you had added to the methods section.

To be transparent, add a supplementary table showing all the models you have fitted, with K, logLik, AIC, etc. It will probably be a long table but it's important to provide full results.

Author response to Reviewer 3: Round 2

The supplementary information seems to be missing from the revised ms.

AUTHOR: Thank you for bringing this to our attention. We confirm that the supplementary information has now been included with this revised submission. In the previous round of review, no modifications were made to the supplementary material, which is why it was not re-uploaded at that stage. We have ensured that the correct and complete version accompanies the current revision for your evaluation.

I still find the model selection analysis somewhat misleading. The reference model keeps changing because you are only comparing models within subsets. For example in table 2, Model p(effort + Elevation + TPI + TWI + TRI), psi(.) is the worst supported model within the batch and yet is is a lot better supported than Model p(effort + Homo), psi(.), which is the best model in another batch. The same thing applies even between different tables: the best model in Table 3 is actually a lot worse than the entire group of models with environmental covariates in Table 2. You need to be quite a careful reader familiar with AIC-based

model selection to notice this.
AUTHOR: Thank you for this important observation. We acknowledge that comparing models only within predefined groups (i.e., environmental, biological, and anthropogenic) led to potentially misleading interpretations of model support, as ΔAIC values were calculated relative to different reference models. Following your suggestion, we have revised our model selection approach to rank *all* candidate models together, regardless of group, ensuring that ΔAIC values are now consistently calculated relative to a single global best model. This change allows for a clearer and more accurate assessment of model support and facilitates more transparent interpretation of the results. The revised and consolidated model selection table is now presented as Table 2 in the main manuscript. We have also updated the results and discussion sections accordingly to reflect this change in model comparison.
My interpretation is that we actually have very little evidence that occupancy is related to any of the covariates. Some of the models with covariates on occupancy are better than the null model, for sure, but they might just be picking up variation in detection that these models don't allow for and that we know are important from Table 2.
AUTHOR: Thank you for this important observation. Following your comment, we revised the model selection process to ensure that all models, regardless of covariate group, are now ranked against a standard reference model. As a result of this unified comparison, the best-supported model includes covariates on detection probability only. We have updated the results and discussion sections accordingly. In particular, we now clearly state that no covariates showed a robust effect on occupancy probability, and we caution against overinterpreting any observed trends. As you correctly noted, some of the occupancy models may simply reflect unmodelled variation in detection, rather than an accurate ecological signal. Nonetheless, since models including environmental covariates consistently performed better, whether linked to detection or occupancy, we retained some ecological interpretation of these variables. However, we have done so with more restraint and explicitly acknowledge the exploratory nature of the analysis and the limitations imposed by the data. We hope this more nuanced approach improves the clarity and credibility of our findings
I understand the data limitations and that you can't look at models with covariates on detection and occupancy at the same time. But I feel the honest thing would be to say that the data are inconclusive about what causes variation in occupancy. At the very least, you need to guide the reader much more carefully.
AUTHOR: Following your suggestion, we revised the discussion section to explicitly state that our data do not provide conclusive evidence on the factors influencing occupancy. While some models with occupancy covariates performed better than the null, we acknowledge that these results may reflect residual variation in detection that was not fully accounted for. We now guide the reader more clearly through the limitations of the inference. We appreciate your emphasis on the importance of transparent interpretation and have worked to ensure that our conclusions do not overstate the findings.
Related to above, in line 205 " Akaike's weight (ωi), which represents the amount of variance described by the top–ranking model compared to all the other models" is not quite correct. It's only compared to models in the same subsection of the table. I think it would be better if it was indeed compared to all models.
AUTHOR: Thank you for pointing this out. You are absolutely right, our previous comparison of Akaike weights (ωi) was restricted to model subsets, which could be misleading. As suggested, we have now restructured the model selection to compare all models together in a unified candidate set. Consequently, Akaike weights are now calculated across the entire model set, allowing for a proper assessment of relative model support.

And, line 206 "...covariate weights were calculated by summing Akaike weights across all models in which a covariate appeared". Here, I assume that you recalculated Akaike weights by treating all fitted models as a single set. Otherwise, the covariate weights would not make sense to me. But then I'm a bit surprised by the results since all models with covariates on occupancy (and constant detection) should have very small weights when properly compared across all models, so the weights can't sum up to very much.
AUTHOR: Thank you for your comment. As in the previous review we retained the ranking division between detection and occupancy models, the cumulative weights for covariates on occupancy resulted in high values. As we updated the model selection process, we also changed the model ranking. Now, covariates on occupancy do not retain meaningful weights (<0.01). We included the cumulative weight for covariates on detection probability which can be found in table 3.
Lines 256 to 265: this entire paragraph needs a big disclaimer that these effects are under the assumption of constant detection probabilities, i.e. ignoring the results of the paragraph immediately before this one.
AUTHOR: Thank you for this important observation. This entire section of the results has now been modified to reflect the new model selection.
I might be overlooking it but I can't find the information on how many models you fitted in total, which you said in your response you had added to the methods section.
AUTHOR: Thank you for pointing this out, we apologise for this oversight. It was indeed missing. We have now included this information in the result section.
To be transparent, add a supplementary table showing all the models you have fitted, with K, logLik, AIC, etc. It will probably be a long table but it's important to provide full results.
AUTHOR: Following your suggestion, we have added the suggested table in the supplementary material with all metrics for the 50 fitted models. You can find it as supplementary table 3.

Reviewer 3: Round 3 **Date completed:** 22 June 2025 **Conflicts of interest:** None
Recommendation: Accept / Revisions required / Resubmit for review / Resubmit elsewhere / Decline / See comments
REVIEWER: See comments
With regard to our policy on 'Publishing peer review reports', do you give us permission to publish your anonymised peer review report alongside the authors' response, as a supplementary file to the published article? Publication is voluntary and only with permission from both yourself and the author. Yes/No
REVIEWER: Yes
Comments to the Author: I have read the revised manuscript and feel that the authors have adequately addressed the remaining issues now.

Appendix 1: Reviewer 1's comments on original manuscript (Round1)

Spatio-temporal behaviour of the brown hyena (*Parahyaena brunnea*) in the Fish River Canyon, Namibia: New ecological and conservation insights

Abstract

The brown hyena (*Parahyaena brunnea*) is inherently challenging to study owing to its secretive nature and strictly nocturnal activity. Most studies investigating brown hyenas' ecology and behaviour are over a decade old, despite growing pressure to intensify conservation efforts. Available literature predominantly examines the dietary overlap with co–occurring predators, emphasising the species ecological role as a scavenger, whilst research focused on the species' spatio–temporal behaviour remains limited. To address this gap, we used camera trap data from a survey conducted in Southern Namibia to investigate the effects of different biotic and abiotic factors over the species' occupancy and detection probability, as well as the activity rhythm and temporal overlap between *P. brunnea* and other co-occurring species, including humans. Brown hyena's occupancy and detection probability were mainly shaped by environmental factors. The species showed a preference for the upper plateau and was more easily detected in secondary canyons leading to the uplands. Human activity did not influence occupancy, though we detected a clear temporal partitioning. Brown hyenas were most active during the central hours of the night, with a single activity peak suggesting increased foraging effort and a more predatory behaviour, independent of leopard activity patterns. This study represented the first fine–scale investigation of brown hyenas' spatio–temporal behaviour within the Fish River Canyon. Our findings effectively reduce the knowledge gap on brown hyenas' spatial niche and activity within the arid ecosystems of Southern Namibia, characterized by the absence of larger predators and scarcely affected by human disturbance.

Commented [A1]: "Strictly" is a strong word. Brown hyenas are indeed mostly nocturnal, but they can be active during the day in some contexts. I would find another word.

Commented [A2]: US English here but UK English before. Both languages were used throughout the manuscript. Be consistent.

Significance: As a near-threatened and understudied species, the brown hyena represents an ideal candidate for investigating the spatio-temporal behaviour of a large carnivorous species in a complex arid ecosystem. Findings from this study fill the knowledge gap on the species ecology and highlight the importance of accounting for different abiotic and biotic factors when investigating highly adaptable elusive species. Moreover, we advise conservation and management programmes to account for both sympatric predator and prey species when planning conservation strategies considering that the ecological role of brown hyenas may shift from exclusive scavenger to predator.

Key words: Brown hyena, occupancy probability, activity, camera trapping, carnivore.

Figures and tables located after the main text.

Supplementary material located after reference list.

Introduction

In Southern Africa, biodiversity is declining proportionally to human expansion.[1] Carnivore decline is particularly pronounced in South Africa and Namibia compared to other adjoining countries, with species from the Hyaenidae family experiencing the most significant losses in the region.[2] These species face various threats, with habitat loss and human-wildlife conflict among the main factors leading to population decline.[3]

Among the Hyaenidae family, the brown hyena (*Parahyaena brunnea*), with an estimated minimum range of 4365 – 10 111 mature individuals and a population showing a stable trend, is globally classified as Near Threatened by the IUCN.[4] Indeed, the species has significantly reduced its historical geographical range over the last century.[5] Currently, *P. brunnea* is extant in Angola, Botswana, Namibia, South Africa, and Zimbabwe[4], with Namibia alone hosting nearly one–third of the species' global population[3]. Although the local population trend is deemed stable, the species faces various increasing anthropogenic threats across the country.[4]

Brown hyenas are inherently challenging to study owing to their secretive nature and strictly nocturnal activity[6], which often results in their being overlooked in wildlife research. Compared to other co–occurring large carnivores such as leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*), brown hyenas have been scarcely studied.[7] Indeed, most research investigating brown hyenas' ecology and behaviour is over a decade old, despite growing pressure to prioritize conservation efforts towards the species[3,4].

Commented [A3]: Same comment as above about "strictly nocturnal". See Lemerle MA, Wiesel I, Somers MJ (2024) Recommendations for the development of a carnivore viewing site at a colony of Cape fur seals (*Arctocephalus pusillus pusillus*) in southern Namibia. *Journal of Ecotourism*: 1–18. Online: 10.1080/14724049.2024.2307363. – shows that brown hyenas can be active during the day at the seal colonies.

Most of the contemporary literature on brown hyena focuses on the dietary overlap between the scavenger and co–occurring predators[8,9]. Research focused on the species' spatio–temporal behaviour is still widely overlooked, with inconsistent results about the effect of biotic and abiotic factors shaping the species' habitat requirements. Several studies have reported a positive relationship between the presence of brown hyenas and other sympatric large carnivores[8–11], as expected by the hyena's trophic role as a scavenger seeking feeding opportunities in left–over carcasses[6]. Although there is some evidence to sustain these conclusions, it is essential to underline that (*i*) results from other studies[6,12] are controversial, (*ii*) many studies[6,9,13] have been conducted across different countries characterised by different ecological contexts, and (*iii*) the brown hyena's spatial ecology is, to the best of our knowledge, still largely understudied.

Commented [A4]: Can you elaborate on this? Why are the studies controversial? Or do you mean that both authors have observed opposite things?

In Namibia, most studies on brown hyenas have been performed along the coast and in Northern and Central continental regions[12,14,15]. Considering the ecological plasticity of brown hyenas[6,16], gathering data along its geographical range to understand its adaptability to various ecological contexts is of paramount importance.

In this study, we explored the spatio–temporal behaviour of the brown hyena through a camera–trapping survey conducted in the Fish River Canyon, Namibia. This area marks the Easternmost limit of the Southern recorded national distribution range of the brown hyena[4]. Understanding the species spatio–temporal behaviour is crucial for obtaining insights into its spatial ecology, enhancing its preservation for a future dispersion to the East. Here the species has not been recorded in recent years, likely due to the heightened conflict with small–stock livestock farmers[3].

Specifically, we aimed to (1) determine the influence of environmental, biological, and anthropogenic factors on brown hyena's occupancy and detection probability, (2) investigate the activity rhythms and temporal overlap between the brown hyena and other co–occurring large predators (i.e., leopard), potential prey (i.e., springbok (*Antidorcas marsupialis*), and Leporidae (i.e., *Lepus capensis* and *Pronolagus* sp.)), and humans.

Considering the species' ecological role[6], we predicted that the brown hyena's occupancy probability would be positively affected by the leopard's relative abundance, reflecting the positive interaction between these two species[13]. Accordingly, we anticipated significant overlap in the activity patterns of the two predators as brown hyenas actively seek scavenging opportunities from leopards[8]. We also expected that the relative abundance of prey species would positively affect brown hyena's occupancy probability, as they might seek feeding opportunities both through direct hunting and, indirectly, through scavenging. We predicted low temporal overlap between predators and prey, reflecting a common anti–predatory strategy[17]. As for anthropogenic disturbance, we predicted a negative impact on brown hyena's occupancy probability along with a low temporal overlap with humans on foot and vehicles, given the elusive nature of the species and the already known negative effects induced by human presence[13,18]. Furthermore, we included key habitat and topographical indexes in the analysis to account for the environmental complexity of the study area (i.e., the clear ecological and geographical gradient between upland and lowland areas). As the effect of environmental variables on brown hyena's occupancy probability greatly depends on habitat types[19], we predicted an uncertain directional effect of Topographic Position Index (TPI), Topographic Ruggedness Index (TRI) and Elevation. Finally, for Topographic Wetness Index (TWI), we anticipated a positive effect, as brown hyenas use drainage lines for movements across areas[20].

Materials and methods

Study area

The study was carried out in the Canyon Nature Park (- 17°35'E; 27°26'N, datum WGS84; hereafter CNP), a privately owned protected land located within the Greater Fish River Canyon Landscape (GFRCL) in South–West Namibia (Figure 1). The property covers an area of approximately 450 km^2, neighbouring the /Ai-/Ais Richtersveld Transfrontier Park along its South–Western and South–

Commented [A5]: I think it would be good to elaborate on the loss of brown hyenas in the eastern regions. Did they go extinct? When? Do we know what the population was previously (resident groups or just transient animals? Densities?)? Give more details about this. "recent years" is also not precise enough.

Also, the link is not very clear between "understanding the spatial ecology" and the dispersion to the East. Can you be more precise about how the results from your study will contribute to the repopulation of brown hyenas in the eastern regions?

Commented [A6]: Are leopards the only co-occurring large predators? And springboks and hares the only prey? You wrote predators in plural but only cite leopards. Did you mean e.g. instead of i.e.?
Maybe this is mentioned later, but it would be interesting to have a bigger picture of what species are present in the area.

Commented [A7]: I would start directly at "we predicted that…" and remove the first part of the sentence. You explain the ecological role in the following sentence.

Eastern boundaries, and five privately owned farms. CNP was established in 1995 by acquiring several neighbouring areas intended for livestock farming and hunting. From its foundation, CNP has been dedicated to sustainable tourism, wildlife conservation, and research practices. The property can be divided into two topographically distinct areas (i.e., the upper plateau and the main canyon) separated by an elevation gradient ranging from 400 to 500 m. The area encompasses several mountain ridges, rocky outcrops, plains, riverbeds, and drainage lines. The mean annual rainfall varies between 0–100 mm, with average annual temperatures ranging from 16 to 20 °C.[21] The flora of the region is dominated by formations of dwarf shrubs interspersed with woody vegetation along riverbeds and kloofs, reflecting the typical landscape of the Nama–karoo biome, which covers the Northern areas of the GFRCL.[21]

The mammalian diversity and composition has been severely altered during the last century due to the eradication of larger predators such as lions (*Panthera leo*) and spotted hyenas, and the indirect killing of scavenging species through poison and non–selective traps[22]. However, a consistent recovery of mammals has been taking place since the protected areas were established. To date, the carnivore guild comprises leopards, cheetahs (*Acinonyx jubatus*), brown hyenas, aardwolves (*Proteles cristata*), black–backed jackals (*Lupulella mesomelas*), African wild cats *Felis lybica*, caracals (*Caracal caracal*), honey badgers (*Mellivora capensis*), small–spotted genets (*Genetta genetta*), Cape foxes (*Vulpes chama*), striped polecats (*Ictonyx striatus*), and Cape grey mongooses (*Herpestes pulverulentus*).

Commented [A8]: Due to conflict on the neighbouring farms?

Commented [A9]: When? In 1995?

Commented [A10]: Nice, this answers my comment from above. Can you maybe also cite the main prey species present?

Data collection

From May to October 2023, 42 camera traps have been placed in the field: 36 Wosports Mini Trail and 6 Bolyguard SG520. Each camera trap site was located at a minimum distance of two kilometres from each other to guarantee the independence of each site while taking into account the home range size of the target species.[23] The total sampling area covered about 302 km^2, calculated through the Minimum Convex Polygon (Figure 1).

Owing to the expected low density of the target species, detection probability was maximized by preferentially placing cameras along game paths, forced passages, marking spots, roads, riverbeds, natural springs, and artificial waterholes.[23] To include the topographical variability of the study area in the sampling design, cameras were evenly distributed between the plateau and the canyon areas. Cameras were placed at 30–40 cm above ground, at 2–4 m distance from the target spot, and secured with straps on rocks or trees, following the protocol for medium to large–sized mammals[23]. All cameras were set to operate 24h per day, recording a sequence of three pictures with a five–minute interval between bursts. Camera sites were checked every 26–30 days to download data, check their functionality, and replace the rechargeable batteries.

Commented [A11]: Why 5 minutes? Studies sometimes use 1 min interval. Do you have a reference for that?

Data analysis

All the analyses were implemented in the software R, version 4.3.2[24]. Photos filtering and species identification was performed manually. To reduce pseudo–replication bias, all observations of the same species at same site, which spaced less than 15 minutes between each other were collapsed in one single event, defined as 'independent detection[23]. All images were filtered to obtain an all–species dataset of independent detection events using the 'camtrapR' package in R[25].

The naïve occupancy and the Relative Abundance Index (RAI)[26] were calculated for all species. The naïve occupancy was calculated as the number of detection/total number of camera sites, while the RAI as follows:

$$\mathrm{RAI_i} = \frac{n\ detection}{sampling\ effort} \times 100 \text{ camera nights}$$

Where *i* represents the *i*th covariates, *sampling effort* is the total number of camera–trap days at each camera site, *n detection* is the sum of the independent events for the target species at the corresponding site, and *100 camera trap nights* is a unit of standardization for data comparison.

A binary matrix of detection/non–detection events (i.e., 0 = non–detection, 1 = detection) was created for the brown hyena for each camera site and day (i.e., 24 h camera activity). Thereafter, the dataset was discretized by grouping the camera days into sampling occasions of five consecutive days each.[17] To assess the species occupancy and detection probability we ran single–season single–species occupancy models (SSOMs)[27] implemented in the 'unmarked' R package[28]. Because many mammalian species exhibit seasonal patterns in their behaviour in relation to changing environmental/ecological conditions and since data were collected during one season (i.e., dry season), the closure assumption of occupancy models was not violated. Therefore, findings were interpreted in terms of probability of occupancy[27]. To account for the unbalanced sampling effort among cameras, the variable "sampling effort" was included in the occupancy models as a survey covariate to explore its effect on the detection probability.

Three key categories of site covariates were selected for the analysis: environmental/topographical, biological, and anthropogenic. To encourage the maximum likelihood estimate of parameters, all covariates were standardized at *z*–scores using the *mutate_at* function in the 'dplyr' package[29].

Environmental covariates were extracted using the QGIS (v. 3.28.0) open access software and SAGA GIS (v. 7.8.2). Covariates were extracted starting from the Namibia Digital Elevation Model (DEM)[30] Shuttle Radar Topographic Mission, at 30 m spatial resolution, using the geoprocessing tools found in the SAGA NextGen Processing provider (9.1.0).

Covariate selection was made based on the information reported in the available literature[6,13,16,18,31] and the ecological needs of the target species. Four suitable environmental covariates were selected to test the occupancy probability: (*i*) Elevation, (*ii*) TPI calculated as the difference between a central pixel and the mean of its surrounding cells[32], (*iii*) TRI which conveys the amount of elevation difference between neighbouring cells of a DEM, a proxy for topographic heterogeneity[33], and (*iv*) TWI which conveys the relative wetness or moisture conditions of a landscape based on its topography[34].

Biological and anthropogenic covariates were calculated as RAIs at each camera site. The leopard was included as sympatric top predator. RAIs of springbok and Leporidae were included as potential prey species[8,12,35]. Anthropogenic disturbance was divided into "humans" and "vehicles" to account for the species sensitivity towards different human activities[13,18]. Predicted effects of covariates on brown hyena's occupancy probability are summarized in Table 1.

Commented [A12]: Compared to your list of present carnivores above, can you elaborate a bit more why you only chose to include leopards in your analysis (why not cheetahs for example)? You can also do the same for prey species.

Commented [A13]: I am not sure that this table is necessary. It is redundant with the last paragraph of your introduction. If you have results that differ from your hypotheses, you can mention it directly in the discussion.

Multicollinearity among covariates was tested through the Variance Inflation Factor (VIF), implemented in the 'usdm' R package[36], and considering a VIF ≥ 3 to indicate severe collinearity among convariates[37]. The null model was created by keeping both detection probability (p) and occupancy probability (Ψ or *psi*) constant, to explore the contribution of each covariate in the overall model performance. The most parametrized SSOMs for both occupancy and detection were created by maintaining Ψ and p constant, respectively (see Supplementary table 1). Covariates were divided into key categories and tested separately for Ψ an p to avoid model overfitting. Consequently, detection and occupancy models were tested for environmental biological, and anthropogenic covariates.

All saturated models were tested for *goodness–of–fit* using the *parboot* function implemented in the 'unmarked' R package[28] based on the chi–square statistic, to reproduce the parametric bootstrap method for fitted models set at 1000 replicates. The most complex models were then simplified following the *principle of parsimony* by removing non–significant covariates at each step.

Model selection was based on the Akaike Information Criterion (AIC)[38] and ΔAIC[39] using the *model.sel* function implemented in the 'MuMIn' R package[39]. For both detection and occupancy, models were ranked according to their AIC value against the null model. Models with ΔAIC < 2 were considered as competitors of the best model.[40] Best model selection was then performed based on the Akaike's weight (ωi), which represents the amount of variance described by the top–ranking model compared to all the other models.[39]

We analysed the temporal activity patterns and overlaps for each pair of target species only when more than 20 independent observations per species were collected.[41] Temporal activity patterns were analysed using the R package "overlap".[42] Then, the Hermans–Rasson uniformity test (r) was calculated using the function *HR_test* in the package "CircMLE"[43] to estimate whether a random activity pattern was exhibited by each species (e.g., Viviano *et al*., 2021[44]). Through the R package "overlap"[45], we also estimated the coefficient of overlap (Δ), measured non–parametrically using kernel density estimates, to quantify the temporal overlap between two distinct activity patterns[46]. The overlap coefficient is defined as the area under the two kernel density curves, and it can range from 0 (i.e., 0% overlap) to 1 (i.e., 100% overlap). We used the "Δ1" coefficient for pairwise comparisons between species when for one of the two species less than 75 observations were available. Conversely, we used the "Δ4" estimator when both species had more than 75 records.[41,46] Temporal overlaps were considered as "very low" with $\Delta \leq 0.35$, "low" if $0.35 < \Delta \leq 0.50$, "moderate" if $0.50 < \Delta \leq 0.75$, "high" if $0.75 < \Delta \leq 0.90$, and "very high" if $\Delta > 0.90$.[47] The overlap coefficients' 95% confidence intervals (hereafter, 95% CIs) were estimated through bootstrap resampling (10 000 replicates). The Mardia–Watson–Wheeler test (W) was applied using the R package "circular"[48] to assess whether statistically significant differences among the activity rhythms of the two species were present. Additional bootstrap analysis was implemented to estimate "the probability that two sets of circular observations come from the same distribution"[49], using the function *compareCkern* in the R package "activity". Considering each camera–trap day, using the function *getMoonIllumination* of the R package "suncalc"[50], a chi–square *goodness–of–fit test* was used to detect if records of each species were evenly distributed throughout the moon phases[44]. Lunar phases were classified following Raimondi et al.[51] Lastly, sunrise and sunset mean values for our camera trap survey period were calculated using the function *getSunlightTimes* of the package "suncalc"[50], with latitude, longitude, and date as input parameters. Then, sunrise and sunset mean values were then used to classify the species as cathemeral, diurnal, crepuscular (*i.e.*, observations within ±1 hour around sunrise and sunset), or nocturnal, depending on the proportion of observations recorded at day, night, and twilight period.[52]

Results

Each camera worked for an average of 112.47 ± 32.53 days. The total sampling period included 134 days, corresponding to the dry season of Southern Namibia. The realized sampling effort was 5422 camera–trap days (mean ± SE = 129.1 ± 1.79) out of a potential effort of 5556 days. Brown hyenas were recorded at 14 of the 42 stations (naïve occupancy = 0.33). Among the target species, the springbok was the most detected, followed by leporids, humans, brown hyena, and leopard (Figure 2). A breakdown of all RAI and naïve occupancy values for all detected species is reported in Supplementary table 2.

Commented [A14]: SE?

Commented [A15]: I like this table because it gives a good idea of the species present in the area.

None of the variables showed collinearity issues (i.e., VIF ≥ 3) thus all of them were included in the analysis. The best detection probability model considering environmental covariates contained three variables (Table 2). Elevation exerted a significant and positive effect on detection probability (β = 1.15 ± 0.29 *SE*, z = 4.01, P < 0.001), TPI had a significant and negative effect (β = -0.7 ± 0.16 *SE*, z = - 4.31, P < 0.001), while sampling effort showed a negative effect (β = -0.02 ± 0.01 *SE*, z = -2.69, P < 0.01). The best model to predict the detection probability using biological covariates (i.e., RAI for each species) included Leporidae, which exerted a non–significant negative effect (β = -0.31 ± 0.25 *SE*, z = -1.23, P = 0.22) as well as the sampling effort, which instead produced a significant negative effect (β = -0.01 ± 0.01 *SE*, z = -2.45, P = 0.01) (Table 2). The best detection model tested using

Commented [A16]: You did not discuss this result in the discussion.

anthropogenic covariates included *Homo sapiens* exerting a negative non–significant effect (β = -0.37 ± 0.35 *SE*, z = -1.08, P = 0.28), and sampling effort showing a significant negative effect (β = -0.01 ± 0.01 *SE*, z = -2.44, P = 0.02).

The best model to predict brown hyena occupancy probability using environmental covariates included two variables (Table 3): Elevation with a non–significant positive effect (β = 1.76 ± 1.07 *SE*, z = 1.65, P = 0.10), and TPI with a slightly significant negative effect (β = -2.24 ± 1.3 *SE*, z = -1.73, P = 0.08). Elevation obtained a cumulative model weight of 0.96, while TPI had a cumulative model weight of 0.99 (Table 4). The top model to predict the brown hyena's occupancy probability using biological covariates revealed that the Springbok induced a positive, even if non–significant effect (β = 2.59 ± 2.15 *SE*, z = 1.21, P = 0.23) (Table 3). Springbok's cumulative model weight was 0.75 (Table 4). As for the anthropogenic covariates, the findings revealed that the best model was the intercept–only model, thus indicating no significant effects of human disturbance on brown hyena's occupancy probability (Table 3).

Commented [A17]: You did not explain the cumulative weight model in the method section. I think it is great that you included it, so it would help the reader to understand what the cumulative weight means.

The temporal activity analysis revealed that the brown hyena was mostly nocturnal (84.8% of nocturnal detections), while the leopard was cathemeral (48.27% and 34.48% of nocturnal and diurnal detections, respectively). Among the potential prey, the springbok was primarily diurnal (77.6% of diurnal detections), and leporids were overall mostly nocturnal (86.5% of nocturnal detections), Human activity was classified as mostly diurnal (87.84% of diurnal detections), while vehicles were detected mainly during the day and crepuscular hours (80.85% and 15.42% of diurnal and crepuscular records, respectively – Figure 3).

Considering the temporal overlaps in the studied period (Figure 4), we found a "moderate" temporal overlap between brown hyena and leopard ($\Delta 1$ = 0.60; 95% CI = 0.43–0.77), a "very low" temporal overlap between brown hyena and springbok ($\Delta 1$ = 0.21; 95% CI = 0.13–0.28), a "moderate" temporal overlap between brown hyena and leporids ($\Delta 1$ = 0.74; 95% CI = 0.61–0.86), a "very low" temporal overlap between brown hyena and humans ($\Delta 1$ = 0.12; 95% CI = 0.02–0.21), and a "very low" overlap between brown hyena and vehicles ($\Delta 1$ = 0.14; 95% CI = 0.06–0.23).

Discussion

This contribution effectively enhances the knowledge on the brown hyena spatial niche and activity within the arid ecosystems of Southern Namibia, characterized by the absence of larger predators such as lions and spotted hyenas, and scarcely affected by human disturbance. Our study identified the factors influencing *P. brunnea* occupancy probability in the Fish River Canyon system and provided insight into brown hyena's activity rhythm in relation to those of sympatric predator and prey species.

Overall, brown hyenas were detected at approximately one–third of the camera sites, a value comparable to the leopard's naïve occupancy, yielding low RAI values for both carnivores. The low RAI values observed for these two species in the study area confirm the expected low densities of top predators in arid environments[53]. However, abundance indexes derived from camera traps should be cautiously used as a proxy for density estimates of secretive species such as large carnivores.[26]

The best model explaining detection probability indicates that environmental variables significantly influence brown hyena. The positive effect of elevation suggests that the distinct topographical separation between the upper plateau and the lower canyon may drive the species to prefer higher elevations, restricting its movement in the main canyon. Our findings contrast to those obtained by Thorn *et al.*[31] and Williams[18], where they found no evidence of elevation exerting any influence on the brown hyena's spatial ecology. Conversely, studies conducted by Welch *et al.*[16,19] revealed variable effects, suggesting that the species' spatial ecology is likely and mostly driven by individual preferences rather than environmental factors. Furthermore, the negative effect observed for TPI on brown hyena's detection probability suggests that species roams more frequently in valley or canyon bottoms. Similarly, Beier[54] identified canyon bottoms as common travel routes for cougars in Southern California and as possible corridors for population dispersal. Within CNP, deep secondary canyons are prominent features along the margins of the plateau, and the brown hyena may use them as pathways to facilitate movements to and from the plateau, serving as preferred routes to foraging areas. Indeed, the cameras with the highest detection rate were located inside secondary canyons or in close proximity to ones connecting the lowland to the upland. Brown hyenas appear to use the upper plateau for movement across areas and potentially as selected foraging grounds, thus showing a preference for higher elevations. The flat upland areas host the highest densities of ungulates species within CNP, providing less cover for hunting for ambush predators such as the leopard, whilst may facilitate cursorial hunters such as brown hyenas[12].

Commented [A18]: It feels like a word is missing here. "influence brown hyena presence?"

Commented [A19]: It would be interesting to have a note about where can the water be found. Is there only water in the main canyon, or can you also find some in the secondary ones? I know that your models did not seem to show an influence for TWI, but I think it would be worth indicating the presence of water or not.

Commented [A20]: Related to my previous comment. If there is no water on the plateau, do you think that brown hyenas often go down the canyon to drink water? Which could also explain the high detection rate in the secondary canyons? The covariate TWI was removed from the main model but I wonder if it would still be worth analysing anyway? Maybe separately?

Although elevation and TPI ranked high in the model selection, indicating the species' preference for high plateau, the absence of a significant effect on the occupancy probability for both variables reinforces findings from previous studies highlighting the species' adaptability to colonize a wide spectrum of topographically different habitats[8,16,19].

As for biological covariates, the Leporidae RAI ranked high in detection analysis, while the springbok's RAI ranked high in occupancy analysis, though their effect was non–significant. While brown hyenas may respond positively to areas with higher leporids and springbok abundances, it should be noted that the moderate temporal overlap with leporids and the very low temporal overlap with springboks, suggest a fine–scale spatio–temporal avoidance behaviour adopted by prey to reduce the likelihood of predator encounters. The widespread distribution and higher density of springbok compared to other species in the study area may further explain the non–significant effects observed. Additionally, springboks are also predated by other species. Therefore, further research including spatio–temporal analysis of other co–occurring predators across seasons, is suggested to provide further insight.

Previous studies describe human presence as one of the strongest drivers negatively affecting brown hyena's spatial ecology.[13,18] Our results indicated no influence over the brown hyena's occupancy probability. This result may be explained by the fact that, within the CNP, human presence is reduced to a few ecotourism vehicles and trekking parties stretched over a vast area. Tourism activities are concentrated during daytime while negative interactions, which would implicate spatial segregations, such as hunting and poaching, are banned in the reserve. Consequently, a territory overlap is allowed through temporal avoidance, as the animals may adjust their activity patterns to reduce the likelihood of direct encounters with humans[55]. Indeed, we observed a clear temporal avoidance (i.e., very low temporal overlap) between brown hyena and human/vehicle activity rhythms. To the best of our knowledge, no previous studies have examined the temporal relationship between brown hyenas and humans, so caution is warranted when interpreting this result, as other biological factors might be involved in shaping the species' temporal behaviour.

The temporal analysis confirmed the already reported brown hyena's nocturnal behaviour[6], with a clear single peak of activity during dark hours. This last finding differs from previous studies reporting two distinct activity peaks for the species, one early at night and another early in the morning.[12,54] The single broad peak we observed suggests that brown hyenas use dark hours more homogeneously, potentially indicating, as earlier suggested, temporal avoidance of humans and/or increasing foraging effort throughout the night. When brown and spotted hyenas co–occur, their activity patterns are known to strongly overlap, which, as reported in other studies[17,57], suggests the existence of potential opportunistic behaviours (i.e., scavenging on carcasses). Seemingly with lions, spotted hyenas actively seek them out to access larger food items.[6,11] As these larger predators are absent within CNP, brown hyenas can only kleptoparasite leopards or cheetahs. However, the likely low density of these two species based on RAI values, would rarely create scavenging opportunities for the brown hyena, thus forcing the species to find less readily available food sources. This consideration is supported by the observed activity pattern of the brown hyena, revealing its peak before the peak of activity of the leopard. Indeed, other research[17] has shown that scavengers' activity peaks immediately after apex predators' activity, likely because they take advantage of leftover carcasses. Further studies found that the brown hyena's activity rhythm could markedly change depending on both the area and mammal community. Edwards *et al*.[58] found that, in South–West Namibia, the temporal activities of the brown hyena and the leopard were significantly different. Conversely, other studies showed a high degree of temporal overlap between the two predators due to brown hyena's kleptoparasitism on leopard's kills.[57,59]

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In arid environments such as CNP, resource scarcity may intensify competition within the carnivore guild, prompting avoidance behaviours that facilitate coexistence[60]. Combining the results obtained from the two analyses, we suggest that the brown hyena exhibits partial independence from the leopard, and a tendency to engage at different foraging strategies. Brown hyenas are known to display predatory behaviour along the Namibian coast[14] and are reported to hunt significantly more when carrion is scarce[12]. Additionally, subordinate carnivore species are known to occupy the apex–predator niche when larger predators are absent.[9,61] Our findings confirm the ecological plasticity of the brown hyena, which adapts its spatio–temporal behaviour to the local ecological conditions. Through a study conducted on the spotted hyena, Périquet *et al*.[62] suggested that the structure and intensity of intraguild competition can alter foraging strategies, switching from scavenging to hunting. Consequently, as carcasses left by leopards are limited, the brown hyena may have changed its behaviour, switching from mainly scavenger to active hunter and/or scavenger from carcasses died due to non–predatory factors.

Commented [A22]: In different foraging strategies?

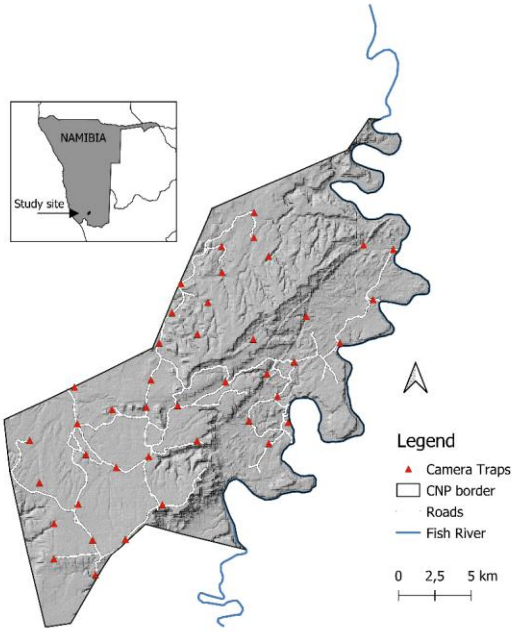
Commented [A23]: I don't really understand this sentence. When did hyenas change their behaviour? Do you mean that they change their behaviour depending on the presence/amount of other carnivores and therefore carcass availability?

This study represented the first fine–scale investigation of brown hyenas' spatio–temporal behaviour within the Fish River Canyon system. We showed that in areas with low densities of predator and absence of larger carnivores, environmental factors might mainly influence brown hyena's spatial behaviour. Nevertheless, we recommend exercising caution when interpreting these results, as it is important to consider variations in elevation between areas, along with other topographic factors.

We suggest that brown hyenas shape their spatial behaviour through the influence of abiotic and biotic factors within CNP, although these effects are dimmed by its ecological plasticity, which ultimately enables the species to inhabit different environments. Data collection across multiple seasons is needed to better define the habitat requirements of the brown hyena within the Fish River system, accounting for the effect of seasonality on species' population dynamics and environmental cycles. We further encourage conservation and management efforts to account for this ecological plasticity, addressing prey availability as well as competition with other carnivores. This is particularly important in light of the proposed reintroduction of larger predators in the Fish River system[22], which could alter intraguild dynamics and potentially reshape ecosystem functioning.

Lastly, our findings indicate that the sustainable tourism model implemented within CNP, which limits human activities to daytime trekking parties, has no significant impact on the brown hyena spatial ecology. We suggest that, as CNP is situated between conservation areas and freehold farmlands, it holds the potential to serve as a safe buffer zone for the species, transitioning from human–dominated landscapes to protected areas. The case of CNP demonstrated that converting farmlands to a privately protected area designated for sustainable tourism may provide significant benefits for wildlife and promote coexistence with humans in Namibia.

Figures and Tables



Source: Digital Elevation Model (DEM) downloaded from RCMRD Open Data Site[30], which is made available here under the Open Database License (ODbL: https://opendatacommons.org/licenses/odbl/1-0/).

Figure 1: Map of the study area (CNP – inset map) and camera trap locations. Abbreviations: CNP = Canyon Nature Park.

Table 1: Environmental, biological and anthropogenic covariates included in the occupancy models. Abbreviations: TPI = Topographic Position Index; TWI = Topographic Wetness Index; TRI = Topographic Ruggedness Index.

Covariates	Predicted effect on occupancy probability	Rationale and supporting literature
Elevation	uncertain	Has been related to brown hyena's occupancy with controversial results.[16]
TPI	uncertain	No information available.

TWI	positive	Indicates riverbeds and drainage lines with thicker vegetation used as ecological corridors by the brown hyena.[20]
TRI	uncertain	No information available.
Leopard	positive	Sympatric top predator, potentially providing food items for the brown hyena and often defined as a key species for brown hyena's presence.[8]
Springbok	positive	Prey species reportedly hunted by the brown hyena and falling within the weight range of its prey preference.[8,12]
Leporidae	positive	Possible prey species, falling within the weight range of its prey preference.[12]
Vehicles	negative	Anthropogenic disturbance, negatively affecting brown hyena's presence.[18]
Homo sapiens	negative	Anthropogenic disturbance, negatively affecting brown hyena's presence.[13]

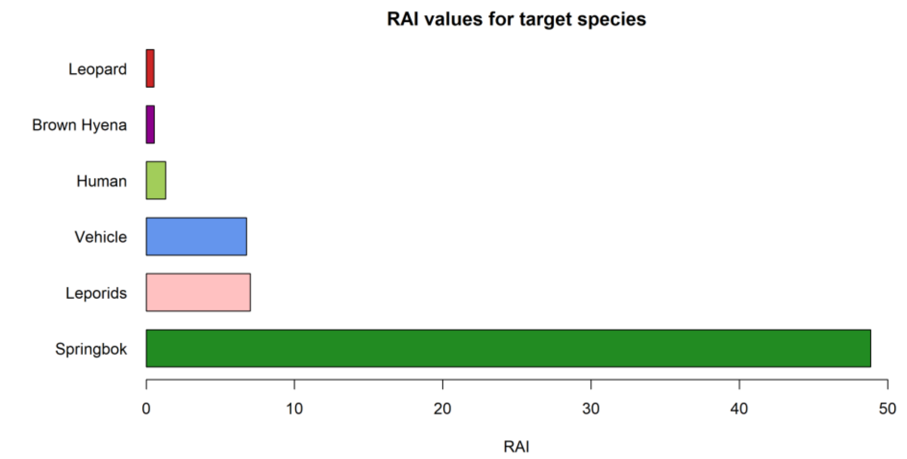


Figure 2: RAI values for all analysed species and vehicles. Abbreviations: RAI = Relative Abundance Index.

Table 2: SSOMs with environmental covariates testing for detection (*p*) with model ranking realized according to the Akaike Information Criterion (AIC). Abbreviations: *psi* = occupancy; AIC = Akaike's Information Criterion; ωi = Akaike's weight; K = number of parameters; logLik = log–likelihood; TPI = Topographic Position Index; TRI= Topographic Ruggedness Index; TWI = Topographic Wetness Index; Homo = *Homo sapiens*. The best model is reported in *italic*, while the null model in **bold**.

Detection models	K	logLik	AIC	ΔAIC	ωi
Environmental covariates					
p(effort + Elevation + TPI), psi(.)	*5*	*-106.03*	*222.06*	*0.00*	*0.42*
p(effort + Elevation + TPI + TWI), *psi*(.)	6	-105.04	222.09	0.03	0.42
p(effort + Elevation + TPI + TWI + TRI), *psi*(.)	7	-104.97	223.94	1.88	0.16
***p*(.), *psi*(.)**	**2**	**-121.47**	**246.94**	**24.87**	**0.00**
Biological covariates					
p(effort + Leporidae), psi(.)	*4*	*-117.40*	*242.80*	*0.00*	*0.54*
p(effort + Leporidae + Leopard), *psi*(.)	5	-117.08	244.17	1.37	0.27
p(effort + Leporidae + Springbok + Leopard), *psi*(.)	6	-116.93	245.86	3.06	0.12
***p*(.), *psi*(.)**	**2**	**-121.47**	**246.94**	**4.14**	**0.07**
Anthropogenic					
p(effort + Homo), psi(.)	*4*	*-117.72*	*243.43*	*0.00*	*0.63*
p(effort + Car + Homo), *psi*(.)	5	-117.59	245.18	1.75	0.26
***p*(.), *psi*(.)**	**2**	**121.47**	**246.94**	**3.50**	**0.11**

Table 3: SSOMs with environmental covariates testing for occupancy probability (*psi*) with model ranking realized according to the Akaike Information Criterion (AIC). Abbreviations: *p* = detection; AIC = Akaike's Information Criterion; ωi = Akaike's weight; K = number of parameters; logLik = log–likelihood; TPI = Topographic Position Index; TRI= Topographic Ruggedness Index; TWI = Topographic Wetness Index; Homo = *Homo sapiens*. The best model is reported in *italic*, while the null model in **bold**.

Occupancy models	K	logLik	AIC	ΔAIC	ωi

Environmental					
psi(Elevation + TPI), p(.)	*4*	*-114.94*	*237.88*	*0.00*	*0.63*
psi(Elevation + TPI + TRI), *p*(.)	5	-114.89	239.78	1.90	0.24
psi(Elevation + TPI + TRI + TWI), *p*(.)	6	-114.89	241.77	3.90	0.09
psi(TPI), *p*(.)	3	-118.89	243.78	5.90	0.03
***psi*(.), *p*(.)**	**2**	**-121.47**	**246.94**	**9.06**	**0.01**
Biological					
psi(Springbok), p(.)	*3*	*-119.91*	*245.82*	*0.00*	*0.45*
***psi*(.), *p*(.)**	**2**	**-121.47**	**246.94**	**1.12**	**0.26**
psi(Springbok + Leopard), *p*(.)	4	-119.68	247.36	1.55	0.21
psi(Springbok + Leopard + Leporidae), *p*(.)	5	-119.54	249.08	3.27	0.09
Anthropogenic					
***psi*(.), *p*(.)**	**2**	**-121.47**	**246.94**	**0.00**	**0.98**
psi(Car), *p*(.)	3	-124.87	255.73	8.80	0.01
psi(Car + Homo), *p*(.)	4	-124.87	257.74	10.81	0.00

Table 4: Cumulative Akaike's weights of covariates tested for brown hyena's occupancy probability. Abbreviations: TPI = Topographic Position Index; TRI= Topographic Ruggedness Index; TWI = Topographic Wetness Index.

Covariate	Summed model weight
TPI	0.99
Elevation	0.96
Springbok	0.75
TRI	0.33
Leopard	0.30
TWI	0.09
Leporidae	0.09
Vehicles	0.01
Homo sapiens	0.00

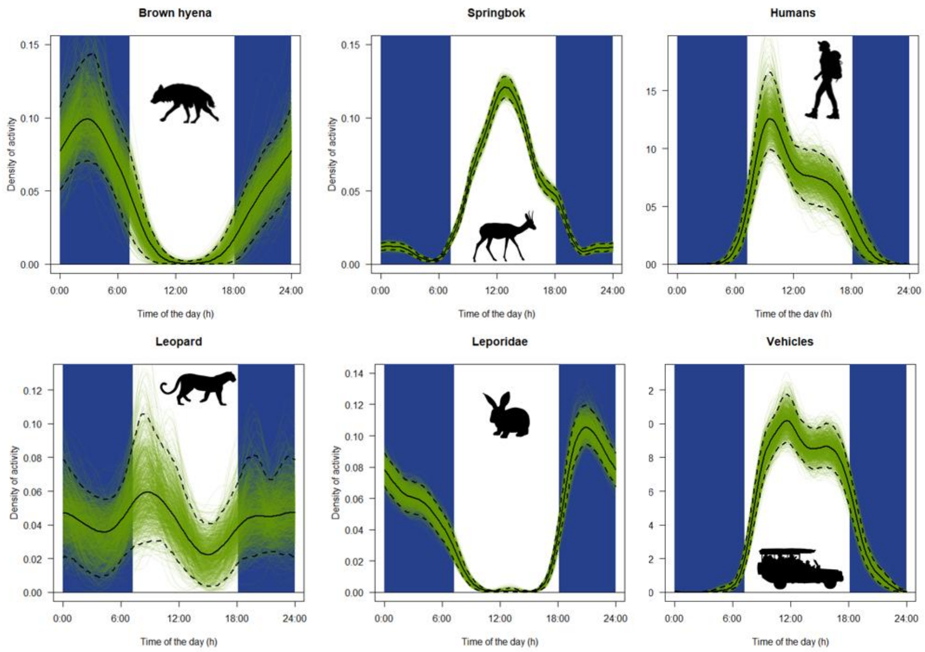


Figure 3: Density estimates of daily activity patterns of the target species. Sunrise is approximately at 7.25, while sunset at 18.17 (solar time). Legend: blue rectangles = dark hours; solid line = activity mean value; dashed lines = 95% Confidence Intervals (CIs); green lines around and inside the dashed lines = bootstrapped estimates of activity patterns.

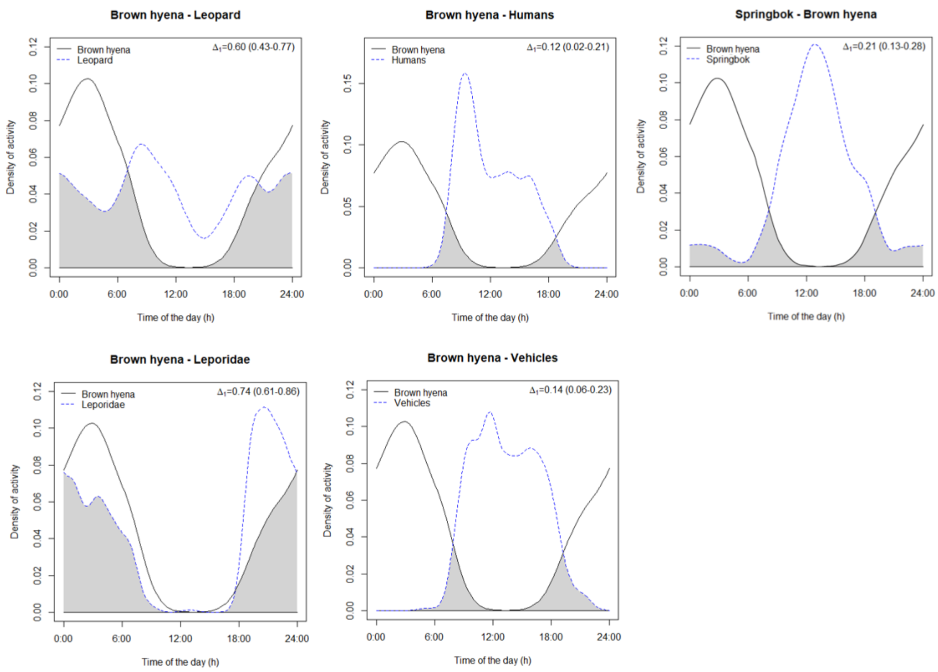


Figure 4: Temporal overlap between pairs of target species. The coefficients of overlap are indicated by shaded grey areas under the two kernel density estimates, and reported along with the 95% Confidence Intervals (CIs).

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Supplementary table 1: Starting models for the occupancy analysis. Abbreviations: *p* = detection; *psi* = occupancy; TPI = Topographic Position Index; TRI= Topographic Ruggedness Index; TWI = Topographic Wetness Index; Homo = *Homo sapiens*.

Null model
p(.), *psi*(.)
Detection models
p(effort+Elevation+TPI+TRI+TWI), *psi*(.)
p(effort+Leopard+Springbok+Leporidae), *psi*(.)
p(effort+Car+Homo), *psi*(.)
Occupancy models
psi(Elevation+TRI+TPI+TWI), *p*(.)
psi(Leopard+Leporidae+Springbok), *p*(.)
psi(Car+Homo), *p*(.)

Supplementary table 2: Record of species (reported in *italics*) and groups (including animal Classes and/or Orders), identified during the camera trapping survey period, along with the number of independent detections, total detection sites, RAI, and naïve occupancy. Abbreviations: RAI = Relative Abundance Index.

Species/group	N. detections	Detection sites	RAI	Naive occupancy
Acinonyx jubatus	3	3	0.06	0.07
Antidorcas marsupialis	2648	25	48.84	0.60
Birds	933	27	17.21	0.64
Lupulella mesomelas	214	32	3.95	0.76
Caracal caracal	9	5	0.17	0.12
Elephantulus sp.	1	1	0.02	0.02
Equus zebra	903	27	16.65	0.64
Felis lybica	42	19	0.77	0.45
Genetta genetta	40	10	0.74	0.24
Giraffa camelopardalis	1	1	0.02	0.02
Herpestes sp.	281	24	5.18	0.57
Homo sapiens	71	14	1.31	0.33

Hystrix africaeaustralis	51	9	0.94	0.21
Ictonyx striatus	1	1	0.02	0.02
Lepus capensis	339	19	6.25	0.45
Mellivora capensis	18	4	0.33	0.10
Oreotragus oreotragus	251	23	4.63	0.55
Oryx gazella	633	30	11.67	0.71
Panthera pardus	28	13	0.52	0.31
Papio ursinus	462	18	8.52	0.43
Parahyaena brunnea	30	14	0.55	0.33
Procavia capensis	279	15	5.15	0.36
Pronolagus sp.	42	7	0.77	0.17
Proteles cristata	26	8	0.48	0.19
Raphicerus campestris	18	7	0.33	0.17
Rodents	25	5	0.46	0.12
Struthio camelus	408	21	7.52	0.50
Tragelaphus strepsiceros	441	28	8.13	0.67
Unidentified	92	30	1.70	0.71
Vehicles	367	14	6.77	0.33
Vulpes chama	6	3	0.11	0.07
Xerus sp.	132	11	2.43	0.26