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Response of a carnivore community to water management in a semi-arid savanna

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ABSTRACT

Water is a limiting and important resource for large herbivores in arid and semi-arid ecosystems. Consequently, provision of artificial water is often used to alleviate limited surface water during dry periods. When foraging, large carnivores benefit from herbivore aggregation around water sources. Large carnivore attraction to areas of high water and prey availability is likely to affect smaller carnivores at these sites through competitive interactions. Here, we explore the effect of water management on the structure and the asymmetric interactions of an African carnivore community using data from camera trapping surveys. We used a functional approach based on four ranks driven by species body size (rank 1: African lions, spotted hyaenas; rank 2: leopards, African wild dogs, brown hyaenas, cheetahs; rank 3: African civets, black-backed and side striped jackals, caracals, honey badgers, servals; rank 4: African wildcats, large spotted genets, striped polecats, mongoose species), and performed multispecies occupancy models and activity pattern analyses. Results show that distance to water influences rank marginal occupancy probabilities with first- and third-ranked species more likely to use sites closer to water while we observed the opposite for second- and fourth-ranked species. However, while marginal occupancy patterns could suggest spatial avoidance, conditional occupancy of a given rank depending on another shows a constant and positive effect of the presence of a higher rank on conditional occupancy of its subordinate rank. Additionally, activity pattern analyses showed some shifts in peaks of activity in some subordinate ranks, although independent from water availability. This work shows that provision of artificial water contributes to shaping the structure of carnivore communities, and we encourage managers to account for these findings. Specifically, ensuring heterogeneity in the distances to waterholes across the landscape will favour a higher diversity of carnivores at the landscape scale.

1. Introduction

In arid and semi-arid environments, surface water is a key and limiting resource for most large mammalian herbivores, especially during dry seasons or years (Redfern et al., 2005; Smit et al., 2007). On several continents, managers have consequently resorted to artificially providing surface water (James et al., 1999; Rosenstock et al., 1999; Redfern et al., 2005) to improve herbivore numbers and distribution.

Surface water provisioning affects herbivore distribution across the landscape with aggregation of water-dependent herbivores around water sources (Valeix, 2011), which, in turn, has the potential to influence the spatial and foraging ecology of their predators (Valeix et al., 2010). Therefore, large carnivores appear to take advantage of the higher availability of large herbivores around water sources. This may have knock-on effects on other species through diverse interactions, and may ultimately affect biodiversity patterns. Incorporating

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anthropogenic effects into our understanding of the functioning of interspecific interactions is important if we want to fully grasp the picture of community functioning worldwide (Dorresteijn et al., 2015). Surprisingly, little is known about the cascading effects of water provisioning on the structure and functioning of mammalian communities.

In particular, carnivores are involved in a rich network of interactions in the carnivore community (between large carnivores, mesocarnivores and small carnivores). Although positive interactions between carnivores exist, such as trophic facilitation through the provision of carrion (Pereira et al., 2013; Sivy et al., 2018), most research reported the extent of negative interactions among carnivores worldwide, ranging from interference competition, such as kleptoparasitism (Péruquet et al., 2015; Balme et al., 2017), to extreme cases of intraguild predation/killing (Palomares and Caro, 1999; Donadio and Buskirk, 2006; Prugh and Sivy, 2020; Curveira-Santos et al., 2021a). The literature on which these studies are based mostly reports a dominance of the larger over the smaller species, and intraguild killing and predation are expected to occur mostly between species of intermediate difference in body size (Donadio and Buskirk, 2006; Prugh and Sivy, 2020). Changes in the behaviour of smaller carnivore species in response to the fear of encounters with dominant species are widespread (Broekhuis et al., 2013; Vanak et al., 2013), and these fear-driven effects together with the lethal effects of larger carnivores (killing) may lead to the suppression of smaller carnivores (Ritchie and Johnson, 2009). For instance, a comparative study across several reserves in South Africa revealed that the presence of African lions (*Panthera leo*) is associated with a numerical reduction and a lower diversity of the mesocarnivore community (Curveira-Santos et al., 2021b).

How water distribution in general, and the artificial provisioning of surface water in particular, affects the structure and the functioning of the mammalian carnivore community is a little investigated topic. However, because the presence of water influences the abundance and distribution of large carnivores, through large herbivores, it may have negative consequences for sympatric smaller carnivore species. Indeed, because water is a spatially fixed resource, a common concern pertaining to artificial water provisioning, is the potential increase in the number and strength of interspecific negative interactions, such as interference competition or intraguild predation (Rosenstock et al., 1999; Krag et al., 2023). The heightened risk of exposure to lethal intraguild interactions could lead to an increased fear in high water availability areas, and consequently, to the spatial avoidance of these areas by subordinate carnivore species, or to a shift in their temporal activity pattern to minimise the risk of encountering larger carnivores. Such indirect adverse effects of water on smaller carnivores were suspected in a study where African wild dogs (*Lycaon pictus*) were found further from water during a drier year, and where the authors hypothesized that it could be due to the need to mitigate negative interactions with larger competitors (Ndaimani et al., 2016).

The African carnivore community is diverse and characterized by a wide body size gradient. A large body of literature has addressed interactions and coexistence mechanisms between large carnivores (Creel and Creel, 1996; Péruquet et al., 2015; Balme et al., 2017), between large carnivores and smaller carnivores (Kamler et al., 2007; Müller et al., 2022; Curveira-Santos et al., 2021a, 2021b) and, to a lesser extent, among smaller carnivores (Loveridge and Macdonald, 2003; Mills et al., 2019; Easter et al., 2020). Thanks to recent advances in hierarchical models, studies also explored the effects of environmental and anthropogenic variables on carnivore communities (Van der Weyde et al., 2018; Farr et al., 2019; Easter et al., 2020). However, few studies have attempted to integrate and explore asymmetrical interactions between functional groups that affect the carnivore community response to environmental or anthropogenic factors. Using a recently developed multi-species occupancy model (Rota et al., 2016), we explored the potential impact of surface-water provisioning on an entire southern African carnivore community while accounting for the asymmetric relationship between functional groups of carnivores. We developed a

functional approach whereby species were grouped into four ranks (mainly according to carnivore body size, see Table 1 for rank composition), with the first rank corresponding to the largest, most dominant species, while the fourth rank included the smallest, most subordinate species.

Our study is underpinned by the following two interacting hypotheses (Fig. 1):

- 1) Water availability influences the space use of rank 1 carnivores, as they rely on the spatial distribution of their main prey (i.e. large herbivores), which is in turn largely influenced by water distribution.
- 2) Asymmetric negative interactions between functional groups (competition and/or predation), with a rank suffering mainly from negative effects from the direct dominant rank, result in a cascade of negative effects, i.e. rank 1 carnivores have a negative effect on rank 2 carnivores, which in turn have a negative effect on rank 3 carnivores, which ultimately negatively influence rank 4 carnivores. Due to the “hyper-predatory” nature of the leopard (*Panthera pardus*, rank 2, Curveira-Santos et al., 2021a), we also expect rank 2 carnivores to have a negative effect on rank 4 carnivores. As a consequence, subordinate carnivores should seek to avoid these negative interactions, in space (occupancy) and/or in time (activity patterns).

The combination of these two hypotheses led us to formulate the following predictions. First, we expect rank 1 carnivores, as the dominant carnivores, to display higher occupancies and optimal activity patterns (i.e. no shift from their ‘textbook’ nocturnal activity pattern), in high water availability areas characterized by a high prey availability. In response, in these high water availability areas, we predict a lower occupancy of rank 2 carnivores and/or a shift in their activity pattern to minimise their exposure to potential negative interactions with rank 1 carnivores. In turn, rank 3 carnivores should benefit from the expected lower occupancy level of rank 2 carnivores, and display a higher occupancy close to water. Rank 3 carnivores should also adjust their activity patterns to minimise exposure to rank 2 carnivores. Finally, and following the same logic, rank 4 carnivores’ occupancy should be lower in high water availability areas, and their activity patterns depart from optimum in response to occupancy and activity patterns of rank 3 carnivores. In low water availability areas, characterized by fewer large herbivores and consequently fewer dominant rank 1 carnivores, we expect to observe the opposite.

2. Material and methods

2.1. Study site

Hwange National Park (HNP) is a protected area of ~15,000km² located in western Zimbabwe (19°00’S, 26°30’E) sharing its western border with Botswana (Fig. 2). It is characterized by a semi-arid climate with a mean annual rainfall of ~600 mm and most rains occurring between November and March. As the dry season progresses, natural water sources (rivers and rainfall-fed waterholes) dry up. Since the 1930s, surface water is managed and provisioned through the pumping (either diesel-powered or more recently solar-powered) of underground water, and artificial waterholes have become the main source of drinking water for animals (Chamaillé-Jammes et al., 2007a). Artificial waterholes do not exceed 5 m in depth and are on average slightly <100 m large (Valeix, 2011; Hulot et al., 2019). In most years, the only surface water available in the dry season is found in these artificially pumped waterholes (a few natural pans can exceptionally hold water throughout the dry season in years with a good annual rainfall), which always have water and are permanent sources of water in the ecosystem.

2.2. Camera trap surveys

We analysed data from four camera trap surveys carried-out in the

Table 1
Rank information. Species, body mass (Jones et al., 2009) and detection information.

Rank	Species	Body mass	Non-independent detections	Proportion of non-independent detections	Number of independent detections	Proportion of independent detections
R1	Lion	159	446	0,208	159	0,168
R1	Spotted hyaena	64	1698	0,792	786	0,832
R2	Brown hyaena	43	19	0,038	10	0,040
R2	Cheetah	51	8	0,016	5	0,020
R2	Leopard	52	361	0,725	191	0,770
R2	Wild Dog	22	110	0,221	42	0,169
R3	Aardwolf	8	3	0,005	3	0,008
R3	African civet	12	14	0,025	13	0,034
R3	Black-backed jackal	8	189	0,337	135	0,351
R3	Caracal	12	184	0,328	117	0,304
R3	Honey badger	9	92	0,164	62	0,161
R3	Serval	12	13	0,023	11	0,029
R3	Side-striped jackal	10	66	0,118	44	0,114
R4	Banded mongoose	1	35	0,061	7	0,015
R4	Bat-eared fox	4	56	0,097	47	0,102
R4	Large-spotted Genet	2	34	0,059	24	0,052
R4	Mongoose sp	Unk	5	0,009	4	0,009
R4	Selous mongoose	2	19	0,033	18	0,039
R4	Slender mongoose	1	8	0,014	5	0,011
R4	Striped Polecat	1	46	0,080	40	0,086
R4	White-tailed mongoose	4	37	0,064	36	0,078
R4	Wildcat	4	332	0,577	279	0,603
R4	Yellow mongoose	1	3	0,005	3	0,006

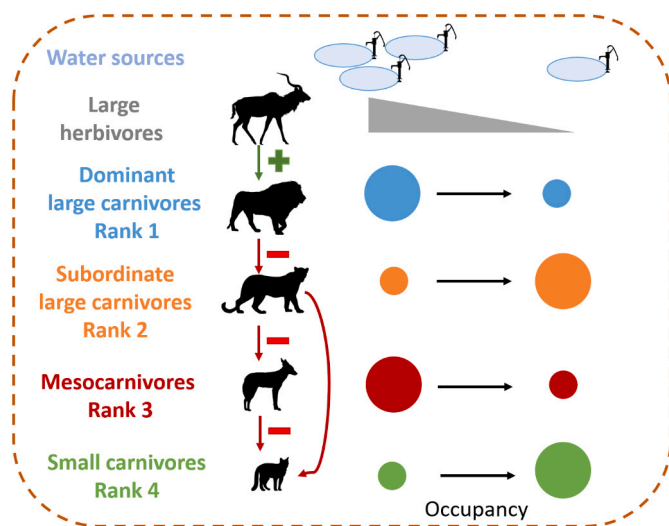


Fig. 1. Representation of the hypotheses/predictions of the study regarding carnivore space use. Within the carnivore community, a dominant rank should have a negative effect on the direct following rank (through an increase level of predation and/or competition). Avoidance patterns should emerge from these negative interactions, and abundance and occupancy patterns should in turn emerge from these avoidance patterns. In high-availability water areas, associated with a higher abundance of large herbivores, rank 1 carnivores should be abundant and occupy numerous sites. This in turn should negatively affect carnivores from rank 2, with associated positive consequences on the third-rank mesocarnivores, which will be released from negative interactions from rank 2 carnivores. Eventually, this should negatively influence small carnivores from rank 4. In low-availability water areas, we expect to observe the opposite. See Table 1 for details on rank composition.

dry season and characterized by contrasting availabilities of surface water. The north-eastern surveys (Ngamo (2014, $N = 41$ stations) and Guvalala (2015, $N = 51$ stations)) have a high density of waterholes, while the south-western surveys (Jozivanini (2017, $N = 40$ stations, including one station with no data) and Shakwanki (2013, $N = 41$ stations)) have a low density of waterholes (Fig. 2). These four surveys are on Kalahari sands, and characterized by similar dystrophic woodland

and bushland savanna (Arraut et al., 2018). To account for a possible edge effect and the potential impacts of human activities adjacent to the park, we excluded 7 camera trap stations localized within 5 km from a border of the park with communal areas (Fig. 2). Camera trap stations were 4-5 km apart, and ran for 48–77 days. They were positioned along roads or game trails to ensure easy access to trap sites but also better detection of carnivores, known to use these features (Abrahms et al., 2016). Camera trap stations consisted of two motion-sensitive cameras (Cuddeback, models 1125, 1149 and C1, Non-Typical, WI, USA; Panthera, model V4, Panthera, NY, USA) at ~100 cm above the ground, facing each other (7-10 m apart) and taking one photo at a time once triggered. Cameras were checked regularly to change SD cards or batteries and recover data.

2.3. Study species

The entire carnivore community was studied. We adopted a functional approach and grouped species primarily according to their body size. Regarding large carnivores (species weighing >15 kg), we have assigned African lion and spotted hyaena (*Crocuta crocuta*) to rank 1 (R1), corresponding to the largest and dominant large carnivores. Leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), African wild dog and brown hyaena (*Hyaena brunnea*), were assigned to rank 2 (R2), as they are smaller and suffer from negative interactions with either lions, spotted hyaenas or both (Creel and Creel, 1996; Hunter et al., 2007; Balme et al., 2017). This ranking is in accordance with Prugh and Sivy (2020). Rank 3 (R3) corresponds to mesocarnivores, whose weight range is 8-15 kg: black-backed (*Canis mesomelas*) and side-striped (*Canis adustus*) jackals, caracal (*Caracal caracal*), serval (*Leptailurus serval*), African civet (*Civettictis civetta*), honey badger (*Mellivora capensis*) and aardwolf (*Proteles cristata*). Rank 4 (R4) corresponds to small carnivores weighing <8 kg: wild cat (*Felis silvestris*), bat-eared fox (*Otocyon megalotis*) and all genet and mongoose species. Rank composition, species body mass, and information on detections are presented in Table 1. Species were identified using TrapTagger (Wildeste AI Conservation, South-Africa, <https://wildesteai.org/traptagger/>), an open-source AI-driven photo-tagging system, at the time under development, assisting in the detection of and counting of animals in images. Then, we used the same system to manually tag the species.

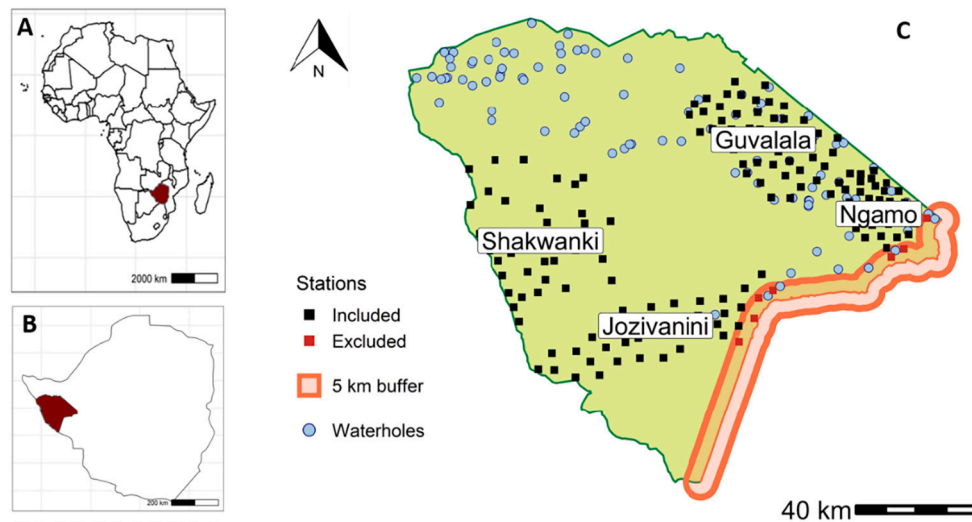


Fig. 2. Locations of (A) Zimbabwe and (B) Hwange National Park in Zimbabwe. (C) Map of camera trapping surveys (squares) and waterholes (circles) and of selected (black) and excluded (red) camera trapping stations, and 5 km buffer zones (orange). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.4. Multi-species occupancy model

2.4.1. Modelling

We fitted the Rota et al. (2016) multi-species occupancy model with penalization (Clipp et al., 2021) using the OccuMulti function and OptimalPenalty argument of the *unmarked* package (version 1.2.5, Fiske and Chandler, 2011) in R. 4.1.2 (R Core Team, 2023) on the four ranks, i. e. instead of looking at individual species responses, we looked at the responses of the four ranks in which species are grouped (see previous section). This “multirank” occupancy model rely on temporally replicated sequences of 0 (rank not detected) and 1 (rank detected) and allows to estimate the marginal occupancy (here, the probability of a site being occupied by a given rank). It further allows estimating the conditional probability, i.e., the probability that a rank occupies a site given the presence or absence of a higher rank. Finally, it allows the modelling of these probabilities as a function of covariates. To determine the best model, we used a 3-step approach. First, we determined the best detection model, upon which all subsequent models were built. In this first step, a constant occupancy model was used, for each rank. Second, we compared different occupancy models to determine which covariates affected rank marginal occupancies. No interaction between ranks was considered in this step. Third, a set of models was built upon the best models from step 2, and included pairwise interactions between ranks, either constant pairwise interactions (i.e. association in space between ranks did not vary with environmental factors), or pairwise interactions dependent on covariates. At each step, we tested a set of covariates of interest and used Akaike Information Criteria (AIC, Burnham and Anderson, 2002) values and a biological rationale to guide our decision about the best biological model among the models with $\Delta_{AIC} < 2$ from the minimum. In all the compared models, we assumed that the covariates affected the detection and the occupancies of all ranks. We preliminarily assessed that occupancy bias was minimized when occasion length was equal or superior to seven days (Appendix A). Accordingly, data were collapsed into one-week temporal replicates giving 11 sampling occasions of seven days across the four surveys.

2.4.2. Model covariates

The detection model included 3 covariates (see appendix C for details on the calculation):

- Habitat structure information (open habitat versus closed woody habitat) at the location of each camera trap station (extracted from Arraut et al., 2018) as a proxy for visibility index.
- The frequency of use by humans was assessed by the Human Relative Abundance Index (HRAI) at each station.
- The camera trapping effort.

Occupancy models included the variable of focus in this study: managed water, but also environmental variables expected to influence site use by carnivores (habitat structure and prey abundance). All artificial waterholes hold water throughout the dry season and their location was extracted from a GIS layer of artificial waterholes in HNP for the period 2013–2019. From this layer, we calculated two covariates: (i) the Euclidean distance to the nearest waterhole, calculated at each station, covering a large gradient of distance to the nearest waterhole (0.098 km to 46,27 km), and log-transformed and (ii) the density of waterholes, calculated for a 10 km buffer around each station and included as a three-level categorical variable: no waterhole (0), low waterhole density (J0, median = 0.0127), and high waterhole density (J median = 0.0127, maximum value = 0.0318). For habitat openness, we calculated the proportion of open habitat in a 1 km buffer. As the raw distribution was skewed towards very low values and contained many 0, which prevented log transformation, the covariate was transformed into a categorical covariate using a threshold of 1 % of open vegetation to obtain balanced classes. Based on Hayward and Kerley (2008) and Sinclair et al. (2003), we determined the following preferred prey weight ranges: 56–550 kg for rank 1, 0.01–40 and 120–140 kg for rank 2, and 0.01–26 kg for rank 3 (see Appendix B for details on prey species). Unfortunately, preferred prey weight range information was not available for rank 4 and likely included very small prey, such as rodents, birds and insects, for which information is not available from the collected camera trap data. We calculated the Prey Relative Abundance Index for ranks 1 to 3 using the same method as described for HRAI. All spatial covariates were obtained using the Sf R-package (version 1.0.6, Pebesma, 2018). Detection and occupancy covariates were tested for correlation using correlation plots and Spearman correlation tests (Appendix C). When a variable could be included as either a categorical or a continuous variable, or when two variables were highly correlated (Spearman coefficient > 0.7), we chose which variable to keep based on model performance results (AIC). All continuous variables were scaled and centred.

2.5. Activity pattern analyses

Changes in space use are not the only behavioural changes carnivores can make to avoid costly interactions. Indeed, carnivores of different ranks may use the same sites (i.e. occupancy may not show variation in space) despite competitor presence, because they use these sites at different times. Therefore, we also looked at ranks' activity patterns using the package *Overlap* (v. 0.3.4, Ridout and Linkie, 2009). We first looked at the degree of overlap within ranks, between two areas differing in terms of water availability: high (Guvalala and Ngamo) versus low (Shakwanki and Jozivanini) waterhole availability (Fig. 1). Either activity patterns were similar (overlap close to 1) and we could conclude that there was no change between areas with different water availability, or the patterns were different (low overlap value), and there

was a need for further investigation. Since we were interested in exploring carnivore interactions, in a second step, we estimated activity pattern overlap between dominant and subordinate ranks at both high and low water availability. An overlap coefficient $\hat{\Delta}$ close to 1 indicated no temporal avoidance between ranks, while a coefficient $\hat{\Delta}$ close to 0 was an indication of complete temporal avoidance between ranks.

3. Results

3.1. Occupancy

We recorded 22 carnivore species (Table 1) and 24 prey species (Appendix B) over 7896 camera trap days across 165 sites. Independent detections, i.e. after applying the 30-min independence threshold,

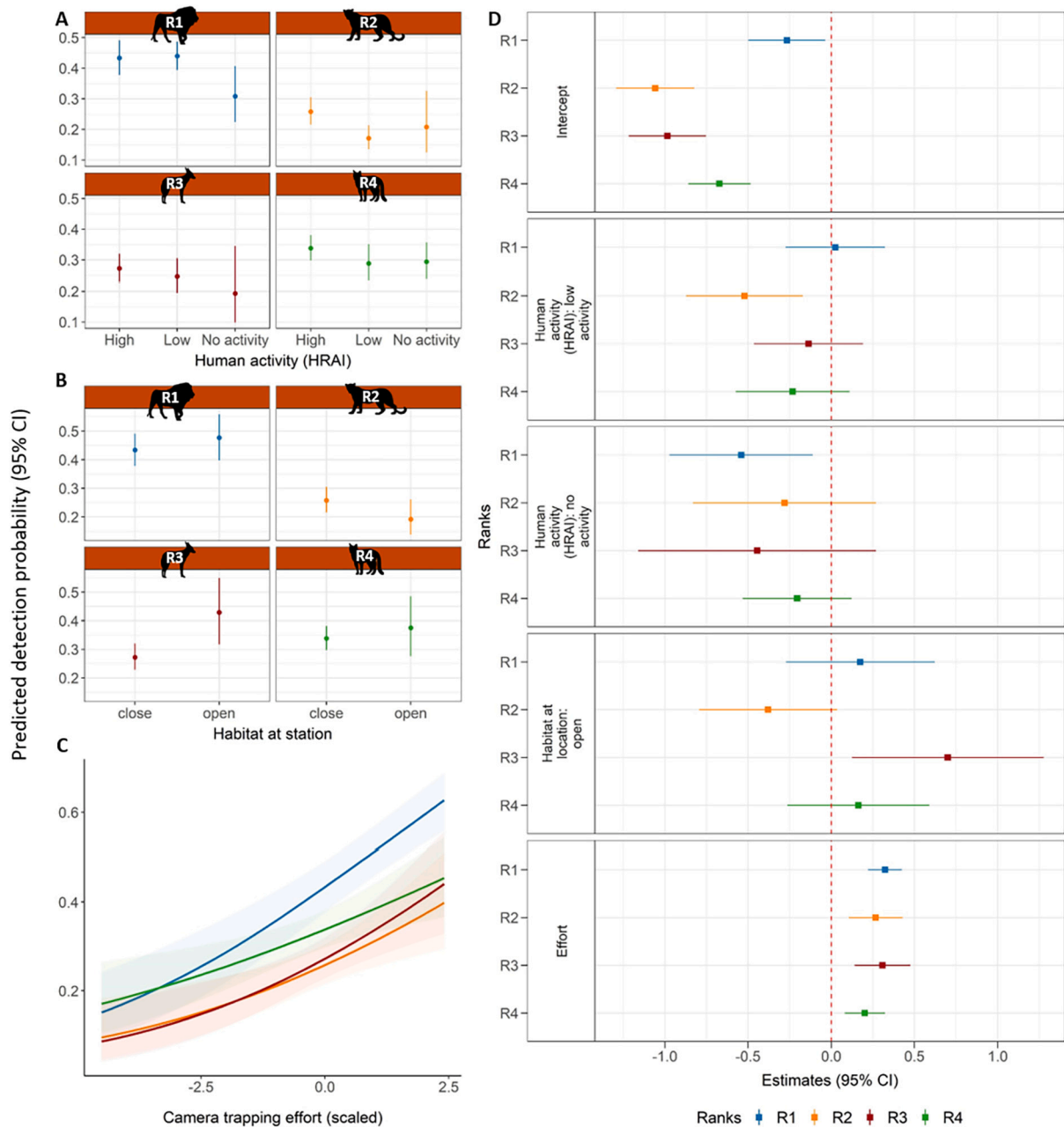


Fig. 3. Predicted detection probability and 95 % confidence intervals of first (blue), second (yellow), third (red) and fourth (green) carnivore ranks as a function of (A) categorical human activity (HRAI), (B) habitat at station and (C) camera trapping effort. For each plot, the other variables are fixed. (D) Effect size of human activity (HRAI: low, high (intercept), no human), habitat at station (open, close (intercept)) and camera trapping effort on rank detection. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

amounted to 15,586 all species pooled, including 2041 carnivore pictures (there were 945, 248, 385 and 463 independent pictures for ranks 1, 2, 3 and 4 respectively). Raw data showed that ranks 1, 2, 3 and 4 occupied 143, 101, 103, 119 sites respectively (see Appendix D for details of occupied sites). While ranks 1, 2, 4 were dominated, respectively, by spotted hyaena, leopard, and wild cat in terms of both independent and non-independent numbers of detections, rank 3 was dominated by two species - caracal and black-backed jackal, which displayed similar detection numbers (Table 1). Details per carnivore species can be found in Appendix E.

Based on AIC, there was only one detection model within $\Delta_{AIC} \leq 2$, which included habitat at the camera trap station, categorical HRAI and camera trapping effort (Appendix F, Table S57). This detection model was used for all subsequent models. The detection probability was higher at sites highly frequented by humans (Fig. 3A,D, Table S58). While first-, third-, and fourth-rank carnivores were more detected at stations located in open habitat, we observed the opposite for second-rank carnivores (Fig. 3B,D, Table S58). Finally, all rank detection probabilities varied positively with camera trapping effort (Fig. 3C-D, Table S58). There was also only one marginal occupancy model within $\Delta_{AIC} \leq 2$, which included the presence/absence of open habitat within a 1 km buffer and distance to the nearest waterhole (Table S59). The effect of these two covariates was therefore included on marginal occupancies for all models testing the association between ranks. Contrary to second-rank carnivores, marginal occupancy probabilities of ranks 1, 3 and 4 were positively correlated with the presence of open habitat (Fig. 4B-C, Table S60). As hypothesized, the marginal occupancy probabilities of first and third ranks were negatively correlated with increasing distance to water, whereas the marginal occupancy probabilities of second and fourth ranks were positively correlated with increasing distance to water (Fig. 5A, C, Table S60). Finally, when exploring whether rank spatial association was constant or varied with environmental factors, the two best models ($\Delta_{AIC} \leq 2$) included constant associations between ranks 1 and 2, ranks 2 and 3, ranks 3 and 4, and the second-best models also included interactions between ranks 2 and 4 (Table S61). Since we were interested in documenting these four rank associations in space, we explored results from the second-best model. However, the association between ranks 2 and 4 likely is the least influential. There is a constant association in space between ranks, suggesting an effect of the presence of higher ranks on lower ranks' occupancies independent of environmental variables. These associations were thus not affected by distance

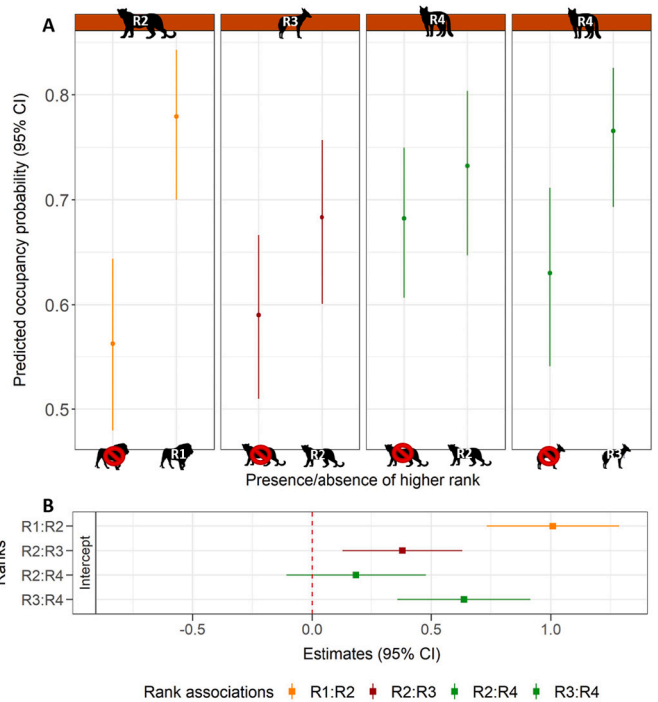


Fig. 5. (A) Conditional occupancy probabilities and 95 % confidence interval of second, third and fourth ranks. The occupancy probability of the rank in each panel is conditional on the presence or absence of a higher rank. For each pair of presence/absence of the two ranks (i.e., we did not exclude sites where other ranks were present). (B) Effect size of presence of a higher rank presence on rank conditional occupancy.

to water. Contrary to our expectations, the presence of higher ranks had a positive effect on the occupancy probabilities of the subordinate ranks (Fig. 5, Table S60).

3.2. Activity patterns

We used the overlap coefficient $\hat{\Delta}$ best adapted when there are at

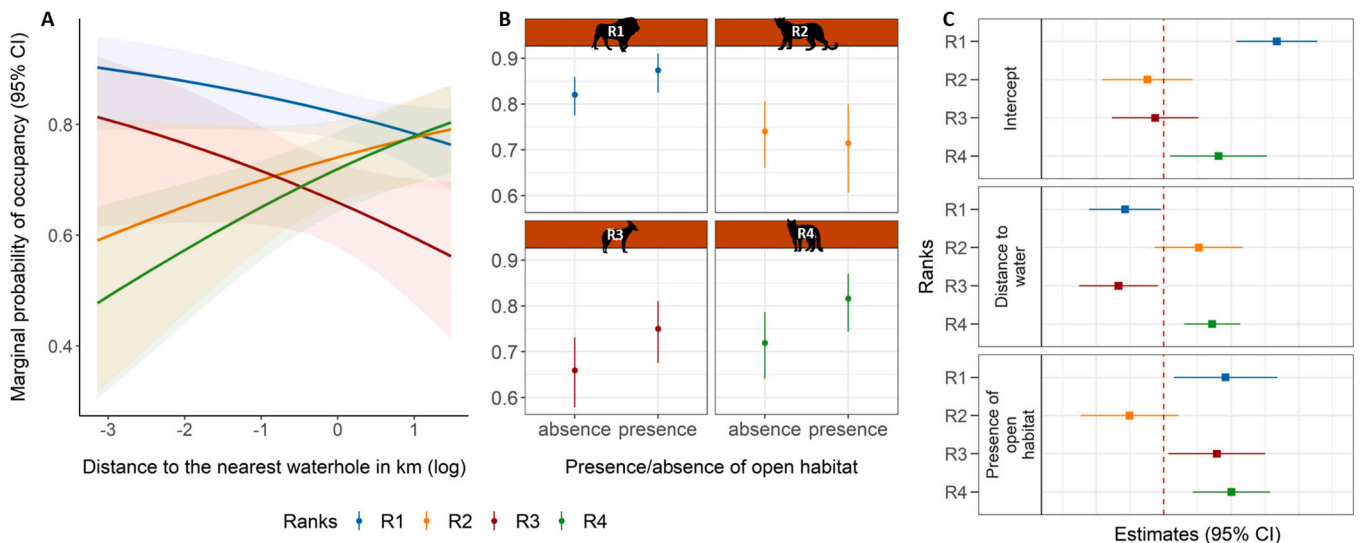


Fig. 4. Marginal occupancy probability and 95 % confidence interval of first (blue), second (yellow), third (red) and fourth (green) carnivore ranks as a function of distance to the nearest waterhole in km (log transformed) (A), and of the presence/absence of open habitat (B). For each plot, the other variable is fixed. (C) Effect size of presence/absence of open habitat (absence (intercept), presence) and distance to the nearest waterhole (log transformed) on rank marginal occupancies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

least 70 detections for each rank in each site (see $\hat{\Delta}_4$ as defined in Ridout and Linkie (2009), Table S62). All ranks displayed nocturnal activity patterns and high overlaps between areas with contrasted water availability, with $\hat{\Delta}$ (95 % CI) of 0.909 (0.865–0.95), 0.85 (0.753–0.937), 0.863 (0.778–0.935), and 0.895 (0.83–0.944) for ranks 1 to 4 respectively (Fig. 6). However, we can observe small shifts in peaks of activity for subordinate ranks (rank 2, rank 3 and rank 4, Fig. 6). While the activity peaks of the second and third rank carnivores shifted towards the end of the night in the high waterhole density area, the activity peak of the fourth rank carnivores shifted towards the beginning of the night (Fig. 6). When we compared higher rank activity patterns with those of lower ranks, we observed high degrees of overlap, with the exception of rank 3 vs. rank 4 in low waterhole density areas and rank 2 vs. rank 4 in high waterhole density areas ($\hat{\Delta} = 0.78$ (0.699–0.861) and $\hat{\Delta} = 0.77$ (0.669–0.851) respectively; Fig. 7). Activity patterns also showed differences in peaks of activity, which could suggest some level of temporal avoidance. However, these differences were present in both low- and high-water density areas, suggesting these shifts were not related to water availability (Fig. 7). Details of activity pattern estimates and confidence intervals are available in Appendix G.

4. Discussion

Even in pristine ecosystems, such as the largest protected areas of the African continent, human imprint is present, and managers have, among other practices, provisioned water to wildlife. While numerous studies assessed the effect of water availability, and hence of surface water provisioning, on herbivore species and communities (Chamaillé-Jammes et al., 2007b; Smit et al., 2007), few investigated its effect on

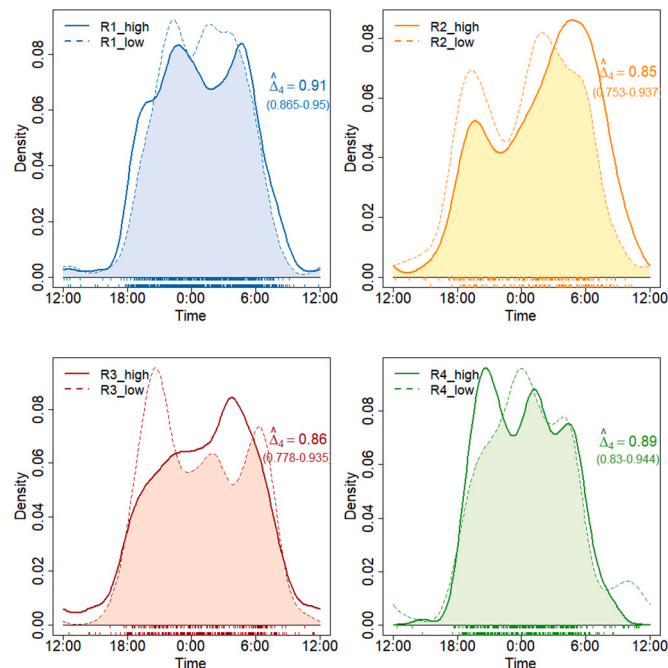


Fig. 6. Kernel density estimates of daily activity patterns of first (blue), second (yellow), third (red) and fourth (green) ranks as a function of time of day. Solid lines correspond to estimates in high waterhole density areas, dashed lines correspond to estimates in low waterhole density areas. Coloured areas represent activity pattern overlaps and coefficients of overlap ($\hat{\Delta}$) and 95 % CI are indicated in each plot. Coefficients of overlap range from 0 to 1. A $\hat{\Delta}$ close to 1 suggests that activity patterns of ranks are similar between areas characterized by contrasting water availability. Conversely, a $\hat{\Delta}$ close to 0 suggests changes in rank activity patterns between the two areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

carnivore species (Valeix et al., 2010; Ndaimani et al., 2016), and even fewer explored its effect on the whole carnivore community (Edwards et al., 2015) in spite of the revolution of camera trapping (Pettorelli et al., 2010) that now allows such investigation.

4.1. Water availability affects the structure of carnivore community

Our results show that carnivore ranks' marginal occupancy probabilities are affected by the distance to water, with marginal occupancies of the first and third ranks decreasing and those of the second and fourth ranks increasing as distance to water increased (Fig. 4A). These patterns support the hypothesis that water availability influences the spatial distribution of the different carnivore ranks and may ultimately influence the structure of the carnivore community. Near water sources, the large dominant carnivores (rank 1) display the highest probability of occupancy (~ 0.90), followed by the mesocarnivores (rank 3; ~ 0.81). The subordinate large carnivores (rank 2) display an intermediate probability of occupancy (~ 0.59) and small carnivores (rank 4) have the lowest probability of occupancy (~ 0.48). This pattern is consistent with our Fig. 1, and could be indicative of spatial avoidance between consecutive ranks. However, far from water sources, all ranks have similar probabilities of occupancy (~ 0.76 , ~ 0.79 , ~ 0.80 for first, second and fourth ranks respectively) except rank 3 carnivores that display a lower probability of occupancy (~ 0.56). This pattern differs from Fig. 1 and could be explained by (1) the lack of strong spatial variation in the dominant large carnivore presence (rank 1) with a high probability of occupancy throughout the landscape, in spite of the decreasing trend as distance to water increases, due to the widespread distribution of spotted hyenas in HNP, which does not seem affected by water (138 sites used over 165, Appendix E), and (2) a scenario whereby the dominant large carnivores (rank 1) are more aggressive towards other large carnivores (rank 2) mainly in areas rich in large prey, i.e., close to waterholes (the highest values of rank 1 prey availability are for short distance to water; Appendix C). Overall, and similarly to other works that already highlighted the consequences of other management practices on carnivore communities (e.g., prescribed burning: Gigliotti et al., 2022), our functional approach shows that the provision of water sources in the landscape has the potential to shape the distribution of carnivore species and hence the structure of the carnivore community.

4.2. Spatial co-occurrence patterns between the functional ranks do not support a spatial avoidance scenario

Ranks' marginal probabilities of occupancy close to water could be indicative of spatial avoidance between ranks (Fig. 1) and one possible explanation for the patterns far from water could rely on inter-rank interactions influenced by the proximity to water. However, conditional occupancy results show that, if there is an effect of the higher rank presence on lower rank occupancies, this effect is constant, does not vary with distance to water (Table S61), and surprisingly is positive (Fig. 5A–B). These results are in opposition with the findings from Brawata and Neeman (2011) where subordinate carnivores avoided areas where dingoes occurred in Australia, or with the hypothesis of Ndaimani et al. (2016) that African wild dogs avoid water due to negative interactions with larger carnivores. Also, they do not support the concern that artificial water may increase interspecific competition (Rosenstock et al., 1999). If the asymmetrical negative interactions between carnivores of different body sizes commonly reported in the literature result in a cascade of negative effects from the most dominant carnivores to the subordinate ones, this does not trigger spatial avoidance of a higher rank by the next lower rank at the scale investigated here. The positive spatial associations of consecutive ranks could be explained by two non-mutually exclusive mechanisms. First, positive interactions, such as scavenging opportunities, also occur in carnivores (Pereira et al., 2013), making intraguild interactions complex (Prugh and Sivy, 2020). Indeed, scavenging is common in species from first to third ranks, such as

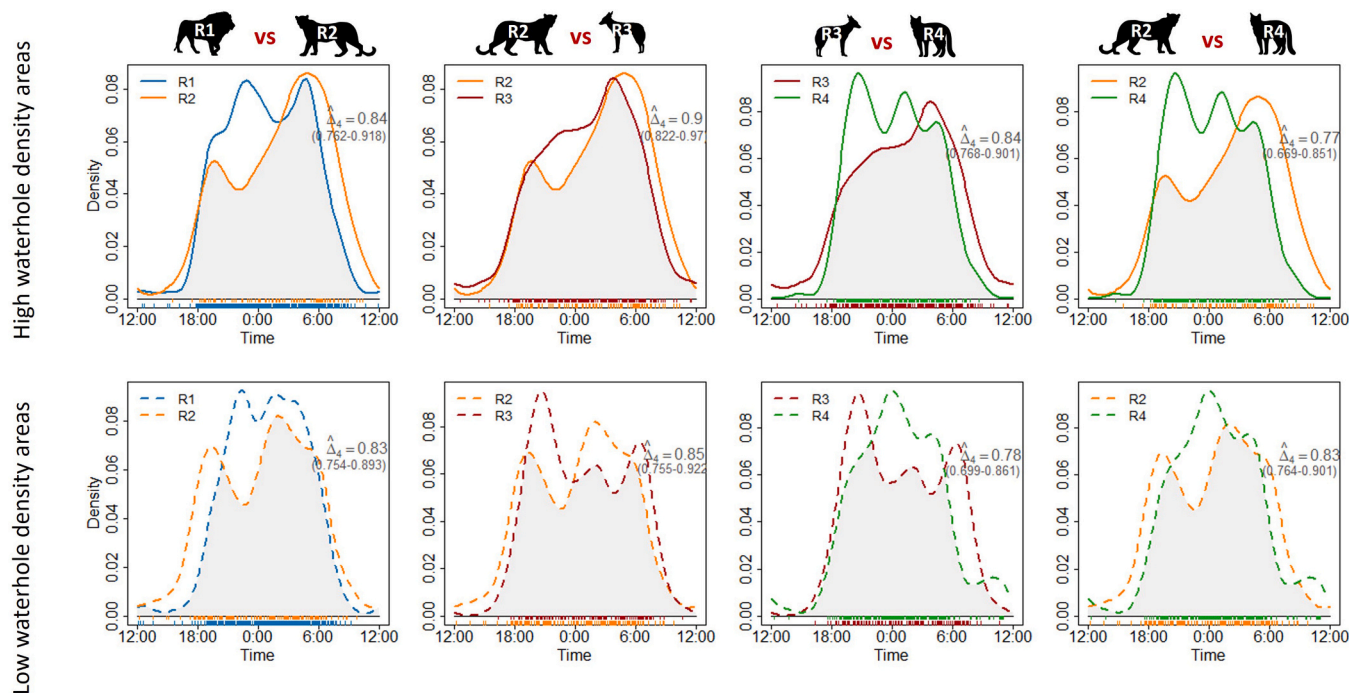


Fig. 7. Kernel density estimates of daily activity patterns for pairs of dominant versus subordinate ranks as a function of time of the day. Solid lines correspond to estimates in high waterhole density areas (higher panel), dashed lines correspond to estimates in low waterhole density areas (lower panel). Grey areas represent activity pattern overlaps and coefficients of overlap ($\hat{\Delta}$) and 95 % CI are indicated in each plot. Coefficients of overlap range from 0 to 1. A $\hat{\Delta}$ close to 1 suggests that there is no temporal avoidance between ranks. Conversely a $\hat{\Delta}$ close to 0 suggests a complete temporal avoidance between ranks.

African lion and spotted hyaena (Péruquet et al., 2015), leopard (Balme et al., 2017), and jackal species (Loveridge and Macdonald, 2003), which are driving the number of detections of their respective ranks (Table 1). As such, the presence of higher ranks could benefit lower ranks through scavenging opportunities, exemplified by rank 3 carnivores benefitting from rank 2 carnivore carrion, in spite of exposing them to a greater risk to be perceived as competitors (“fatal attraction hypothesis”, Prugh and Sivy, 2020). Rank 4 carnivores have a more omnivorous diet, composed of small mammals, birds or insects (Herbst and Mills, 2010), and hence may rely less on scavenging. Besides, carrion provisioning by large carnivores could facilitate ranks 3 and 4 co-existence by lessening the competition pressure over small mammals (Sivy et al., 2018). Altogether, this could explain our conditional model results. However, for ranks 3 and 4, presence of rank 2 carnivores was positively associated with their occupancy, questioning the “hyper-carnivory” status of the leopard (sensu Curveira-Santos et al., 2021a, 2021b). Second, caution is needed when interpreting co-occurrence patterns (Blanchet et al., 2020) and species (or rank) co-occurrences can obviously be driven by other factors, independently of any interaction. This is consistent with the fact that most ranks show a higher probability of occupancy in sites with open habitats nearby and their co-occurrences may result from a shared attraction to such sites (Fig. 4B). For instance, at the species level, honey badgers (rank 3) are indeed more abundant in sites used by large carnivores, as they use similar habitats (Allen et al., 2018). Similarly, and interestingly, in Botswana, occupancy probabilities of carnivores were positively influenced by the detection rate, and therefore presence, of intraguild species (Rich et al., 2017).

The absence of spatial avoidance at the scale investigated here could obviously arise if there is no behavioural avoidance of the immediate superior rank by a lower rank. Still, it is important to keep in mind that avoidance patterns may occur temporally instead of spatially (but see sub-section below) or at finer spatio-temporal scales than the ones investigated here (1 week), in response to an immediate and acute risk of encountering larger dominant carnivores. Cheetahs (rank 2), for

example, tend to use similar landscape areas as lions and spotted hyaenas (rank 1) but avoid them dynamically when the other carnivores are close by (Broekhuis et al., 2013), similar to the adjustments occurring at fine spatio-temporal scales in prey (Latombe et al., 2014). Similar fine-scale avoidance mechanisms were also documented for leopards avoiding lions (Swanson et al., 2016), as well as for caracals avoiding leopard (Müller et al., 2022). Finally, despite active water provisioning, <10 % of HNP is within 2 km from a waterhole (Chamaillé-Jammes et al., 2007a). Therefore, the absence of water immediately available dominates the functioning of the carnivore community. In HNP, lions intensively use the areas close to waterholes but move quickly in areas far from water (Valeix et al., 2010). The intensity of use of a site is indeed not correlated to the probability of occupancy (and not studied here), and this could explain the non-detection of avoidance patterns as subordinate ranks may avoid only sites intensively used by a dominant rank.

4.3. Temporal activity of the functional ranks

It is also possible that rank co-existence is facilitated by temporal adjustments of subordinate ranks. Activity patterns results show that, despite an overall high overlap, those of subordinate ranks differ between high and low water availability areas (Fig. 6), and tend to show small differences with competing rank activity peaks (Fig. 7). Artificial water in HNP is a spatially fixed resource, and carnivore may rely on temporal partitioning as a favoured strategy, rather than spatial segregation, to avoid negative interactions while still benefiting from limiting water resources (Edwards et al., 2015). However, comparisons between ranks indicate that differences in activity patterns happen in both high and low-water-density areas, pointing towards an absence of effect of water availability on rank activity patterns (Fig. 7).

4.4. Originality and limits of a functional approach

Species have been the focus of studies for decades, but recently there

has been an increased recognition of the importance of studying functional groups of species to fully understand the impact of human disturbance on ecosystem functioning (Sundstrom et al., 2012). Our approach defined four functional groups (rank 1: large dominant carnivores, rank 2: large subordinate carnivores, rank 3: mesocarnivores and rank 4: small carnivores), which feed on different prey communities and thus may provide different ecosystem services. It showed that water availability structures the assemblage of these groups in terms of occupancy with areas close to water being largely used by large dominant carnivores and mesocarnivores (to the detriment of large subordinate carnivores and small carnivores). This functional approach further showed that there is no spatial segregation of occupancy between the adjacent ranks. Of course, space use can differ between the different species within a rank (Appendix E), and spatial segregation may occur between species but the diversity of species composing a functional rank may obscure these segregation patterns.

Consequently, the functional approach developed here needs to be complemented with analyses at the species level for a comprehensive understanding.

4.5. Management implications

Climate change is one of the main threats to biodiversity in Southern Africa (Biggs et al., 2008), and increased water scarcity is of high concern in some regions of the continent (Kusangaya et al., 2014; Niang et al., 2014; IPCC, 2021). In addition, mammalian carnivores of all sizes are increasingly threatened worldwide (Wolf and Ripple, 2017, Torres-Romero and Giordano, 2022). In such a context, it appears crucial to understand the effect of water availability, a key environmental resource under heavy human management, on carnivore communities. Whereas increased intraguild competition caused by artificial water provisioning, which can be detrimental to the conservation status of subordinate carnivore species, is a common concern (e.g. Rosenstock et al., 1999; Krag et al., 2023), this hypothesis was not, however, supported by our study. Our work highlighted the potential for waterholes to influence the spatial structure of the carnivore community. Under a whole carnivore community management perspective, and as advised elsewhere (see Sandoval-Serés et al., 2024; but also Harrington et al., 1999 who showed that the decline of roan antelopes (*Hippotragus equinus*) in Kruger National Park, South Africa, was ultimately caused by the establishment of numerous waterholes which precipitated an increase of the zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) populations and hence of the lion population), we encourage managers in similar ecological contexts to favour heterogeneity in terms of distance to water sources in the landscape to help maintain a high functional carnivore diversity at the landscape scale. Indeed, maintaining a sufficient portion of the landscape at intermediate to high distances to waterholes would help supporting carnivore species from rank 2, which includes locally or globally threatened species, such as the cheetah or the African wild dog.

Overall, our study shows that creating and maintaining artificial waterholes has an effect on the carnivore community from a functional viewpoint, as we documented a higher probability of encountering first and third-rank carnivores close to waterholes, than second and fourth-rank carnivores, and these findings should be accounted for when planning for water management in arid and semi-arid ecosystems.

CRediT authorship contribution statement

Aïssa Morin: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Olivier Gimenez:** Writing – review & editing, Methodology, Formal analysis. **Lara L. Sousa:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Justin Seymour-Smith:** Writing – review & editing, Investigation. **Holly O'Donnell:** Writing – review & editing, Data curation. **Marie-Laure Delignette-Muller:** Writing – review & editing, Methodology, Formal analysis. **Daphne Madhlamoto:** Writing

– review & editing, Validation. **Andrew J. Loveridge:** Writing – review & editing, Validation, Supervision, Resources, Funding acquisition, Conceptualization. **Marion Valeix:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors confirm they have no conflict of interest.

Data availability

The code used for the occupancy models, the rank history detection data and the covariates necessary for occupancy models will be made available upon request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110777>.

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