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Spatio-temporal dynamics of African wild dogs in response to larger carnivores in an ecosystem with artificial water provisioning

Elisa Sandoval-Serés [a,b,*], Egil Dröge [a], Marion Valeix [c,d,e], Esther van der Meer [b], Lara L. Sousa [a], Justin Seymour-Smith [a], Andrea Sibanda [a], Elise Say-Sallaz [f], Liz Campbell [a], Duhita Naware [g], Daphine Madhlamoto [h], Roseline Mandisodza-Chikerema [h], Andrew J. Loveridge [a]

[a] *Wildlife Conservation Research Unit (WildCRU), Department of Biology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Tubney OX13 5QL, UK*
[b] *Painted Dog Conservation (PDC), PO BOX 72, Dete, Zimbabwe*
[c] *CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France*
[d] *Long-Term Socio-Ecological Research Site (LTSER) France, Zone Atelier "Hwange", Hwange National Park, Zimbabwe*
[e] *CNRS, Université de Lyon 1, VetAgroSup, LBBE UMR 5558, Villeurbanne, France*
[f] *Population Ecology Research Unit, Mammal Research Institute, Polish Academy of Science, Ul. Stoczek 1, 17-230 Białowieża, Poland*
[g] *Department of Earth Sciences, University of Oxford, 3 South Parks Road, Oxford OX1 3AN, UK*
[h] *Scientific Services Main Camp, Hwange National Park, Zimbabwe Parks and Wildlife Management Authority (ZPWMA), PO Box 5776, Dete, Zimbabwe*

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ABSTRACT

Temporal and spatial partitioning are forms of niche segregation to reduce species competition. Subordinate carnivores can use reactive or proactive strategies to avoid larger predators. We aimed to evaluate if African wild dogs avoid larger predators (leopards, lions and spotted hyaenas) reactively or proactively in space and time at different spatial and temporal scales in an ecosystem with artificial water provisioning in Hwange National Park, Zimbabwe. We used camera-trapping data and generalized linear mixed models, activity pattern overlap, and time-to-event analyses. In general, wild dogs used the same space as the other three larger predators, but at different times. Temporal avoidance of all three predators was especially strong close to waterholes. Spatio-temporally, wild dogs mainly used a reactive strategy to avoid hyaenas, and most likely a proactive strategy towards lions and leopards. Wild dogs were able to coexist at different times in areas (rich in prey) with high aggregation and density of predators (but lower than ~14 hyaenas/100km^2) as long as there was closed vegetation, and enough permanent waterholes (above ~0.01 waterholes per km^2, waterholes being surrogates for prey aggregation and abundance). Conservation management tools should implement heterogeneous waterhole-provisioning schemes to facilitate interspecific coexistence through increasing niche-partitioning opportunities.

1. Introduction

Sympatric carnivores with similar ecological traits often compete over habitat, space and resources (Davis et al., 2018). When one species actively prevents another species from accessing a resource (interspecific interference competition), a form of niche partitioning needs to occur to be able to coexist (Amarasekare, 2002). Temporal and spatial partitioning are forms of niche segregation between competing species, that reduce interference competition and promote coexistence (Karanth et al., 2017; Vanak et al., 2013).

Competition with larger carnivores that are able to dominate smaller ones can shape carnivore communities (Davis et al., 2018; Monterroso et al., 2020). Smaller subordinate carnivores have to balance the trade-off between avoiding dominant carnivores with the need to access key resources (Broekhuis et al., 2013). Hence, balancing this trade-off is crucial for subordinate carnivores to avoid the reduction of fitness caused by the ecological suppression exerted by dominant carnivores (Kozlowski et al., 2011).

Interspecific interactions can depend on scale (Monterroso et al., 2020; Strampelli et al., 2023), as well as biotic and abiotic traits

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* Corresponding author at: Wildlife Conservation Research Unit (WildCRU), Department of Biology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Tubney OX13 5QL, UK.

E-mail address: elisa.sandoval@biology.ox.ac.uk (E. Sandoval-Serés).

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(Pretorius et al., 2021; Vanak et al., 2013). When the density of dominant carnivores increases, subordinate carnivores can diminish the use of prey rich habitats to reduce spatial overlap (St-Pierre et al., 2006), however this could incur energetic costs for subordinate carnivores (Creel, 2018). Additionally, in low prey densities areas, temporal and spatial partitioning can diminish (Karanth et al., 2017). As such, spatio-temporal partitioning can be dynamic and flexible; when there is an increase in temporal overlap, a decrease in spatial overlap can occur, and vice versa (Karanth et al., 2017; Zhao et al., 2020). Overall, landscape and habitat heterogeneity both at local and regional scales tend to promote coexistence (Davies et al., 2021; Manlick et al., 2020).

In arid and semi-arid environments, water is a crucial resource where prey aggregates (Redfern et al., 2003). Consequently, areas close to water (<2 km) are the preferred hunting grounds for carnivores (Périquet, 2014; Valeix et al., 2010; Van der Meer, 2011). As subordinate carnivores face a trade-off between accessing water areas and associated prey, and avoiding dominant competitors, spatio-temporal dynamics are key for carnivore coexistence around water (Atwood et al., 2011; Edwards et al., 2015).

Among large African predators such as lions (*Panthera leo*), spotted hyaenas (*Crocuta Crocuta* - hereafter hyaenas) and leopards (*Panthera pardus*), the African wild dog (referred to as wild dog hereafter) (*Lycaon pictus*) is one of the most subordinate carnivores (Vanak et al., 2013). The wild dog is a highly social and endangered canid (IUCN, 2024). Large dominant carnivores, such as lions and hyaenas, impact wild dogs through intraguild predation, kleptoparasitism, and exclusion from high-quality habitats (Creel, 2001). Wild dogs show strong avoidance both spatially and temporally towards lions (Davies et al., 2021; Swanson et al., 2014; Woodroffe et al., 2017), as lions pose a direct mortality risk to wild dogs (Woodroffe and Ginsberg, 1999). Conversely, the strength of avoidance of wild dogs towards hyaenas and leopards is not as evident (Dröge et al., 2017; Strampelli et al., 2023).

Subordinate carnivores can avoid dominant predators through reactive (small-scale: after detection of an immediate threat) or proactive (large-scale: in response to a priori assessment of predictable and controllable risk) strategies (Broekhuis et al., 2013; Creel, 2018). These avoidance strategies incur costs for subordinate species; proactive strategies will have food-related costs and reactive strategies will have stress-related costs (Creel, 2018; Swanson et al., 2016). Previous studies showed that wild dogs tend to use a proactive strategy mainly to avoid lions but also hyaenas and leopards (Davies et al., 2021; Swanson et al., 2014; Vanak et al., 2013), and wild dogs use a reactive strategy only during the wet season when visibility is low (Vanak et al., 2013).

As niche partitioning can be crucial for the coexistence of wild dogs with dominant predators (Darnell et al., 2014; Dröge et al., 2017) especially around water (Krag et al., 2023; Pretorius et al., 2021), we aimed to evaluate if wild dogs avoid larger competing predators (leopards, lions and hyaenas) reactively or proactively in space and time at different spatial and temporal scales in an ecosystem with artificial water provisioning. In addition, we aimed to determine (taking vegetation characteristics into account) whether seasonality, waterhole density at different spatial scales (as a surrogate covariate of prey abundance), waterhole distance (as a surrogate of prey aggregation) and dominant predators' density affected the avoidance of wild dogs towards large predators in space and time. We expected that wild dogs would neither have attraction nor avoidance towards leopards spatially (1a), but a proactive response (large scale) temporally (1b); that wild dogs would avoid lions using a proactive strategy (large scale) both spatially (2a) and temporally (2b); and finally, wild dogs would avoid hyaenas using a reactive response (small scale) spatially (3a) and a proactive (large scale) response temporally (3b) (Table 1). Furthermore, we expected that wild dogs would have a higher strength of spatial and temporal avoidance (i.e. proactive avoidance or a stronger effect of an avoidance) with the three other predators when there is more water availability in the system (i.e. in the early dry season, close to water, and in areas with higher density of waterholes and large predators).

2. Methods

(a) *Study area*

The study area is in Hwange National Park (HNP), an unfenced protected area in western Zimbabwe (19:00′S, 26:30′E) that covers approximately 15,000 km^2 (Fig. 1). The main habitat types are woodland, bushland and open areas of grassland (this last habitat type is associated to artificial waterholes) (Arraut et al., 2018). The wet season

Table 1
Summary of results: African wild dog avoidance strategy towards predators in an ecosystem with artificial water provision.

Dimension	Scale	Method	Species	Avoidance	Result
Space	Small	GLMM (wild dog number of individuals with predators number of individuals on same location) (Fig. 2)	Leopard (1a)	No	Positive correlation between wild dog abundance and leopard abundance at the same location.
			Lion (2a)	No effect	
			Spotted hyaena (3a)	No	Positive correlation between wild dog abundance and hyaena abundance at the same location.
	Large	GLMM (wild dog number of individuals with predators densities on surveyed areas) (Fig. 2)	Leopard (1a)	No effect	
			Lion (2a)	No effect	
			Spotted hyaena (3a)	Yes	Negative correlation with hyaena density in surveyed areas
Time	Large	Activity overlap (Δ) (Fig. 3)	Leopard (1b)	Sometimes ($\Delta = 0.79$)	Avoidance (different activity pattern) only in the late dry season, in low waterhole density areas, and close to water (<2 km) ($\Delta = \sim 0.70$)
			Lion (2b)	Yes ($\Delta = 0.73$)	Avoidance (different activity pattern) especially close to water ($\Delta = 0.54$)
			Spotted hyaena (3b)	Yes ($\Delta = 0.68$)	
Spatio-temporal	Small	Time-to-event (same location within 1 day) and indices (Fig. 4)	Leopard (1ab)	Not enough data	
			Lion (2ab)	Not enough data	
			Spotted hyaena (3ab)	Yes	Wild dogs detected after longer period after hyaenas than hyaenas after wild dogs (especially closer to water)
	Large	Time-to-event (same location within 8 days) and indices (Fig. 4)	Leopard (1ab)	No effect	
			Lion (2ab)	No effect	
			Spotted hyaena (3ab)	Sometimes	Wild dogs detected after longer period after hyaenas in the late dry season, and the lower the waterhole density

Numbers "1" to "3" and letters "a" to "c" refer to the predictions tested.

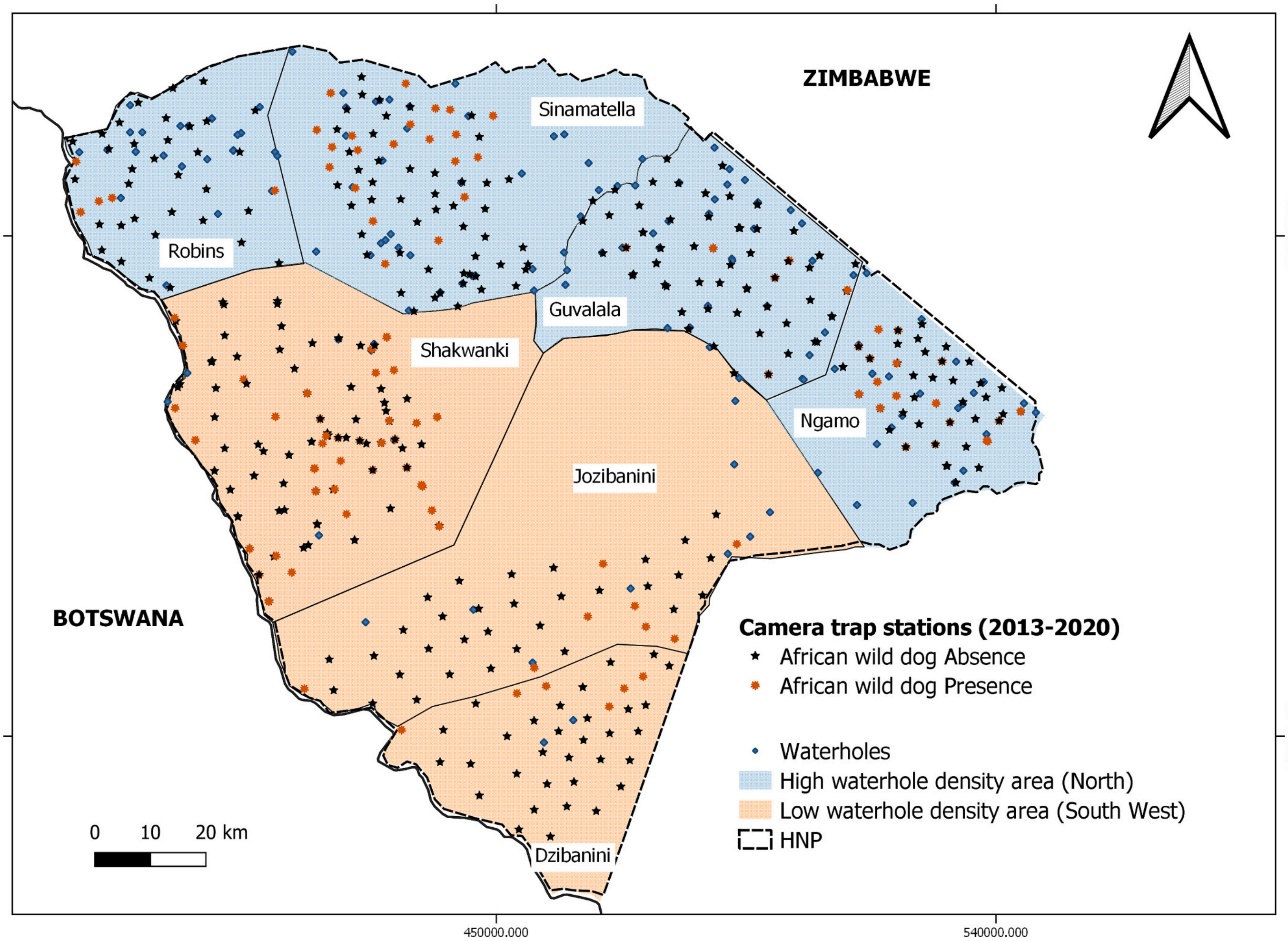


Fig. 1. Map of presence/absence of African wild dogs in the camera trap stations in Hwange National Park, Zimbabwe. Lines divide the surveyed areas of the park.

(November–March) has a mean rainfall of ~380 mm, the early dry season (April–June) has a mean rainfall of ~123 mm, and the late dry season (July–October) has a mean rainfall of ~10 mm (Wilderness Safaris Zimbabwe, unpublished data for 2010–2020). During the dry season (April–October), animals depend mainly on artificial waterholes (which tend to have water the whole year round). Permanent artificial and natural waterholes (containing water even in the late dry season) are predominantly found in the northern area of HNP (North: ~1.69 permanent waterholes/100 km^2; Southwest: ~0.18 permanent waterholes/100 km^2) (Fig. 1, Supporting information, Table S1a). During the study period in HNP (2013–2020), the density of predators was estimated to be in the north of HNP (high waterhole density area): 2.6 (±1.2 s.d.) leopards/100 km^2, 3.5 (±2.2) lions/100 km^2, and 14.1 (±6.0) hyaenas/100 km^2; and in the south west of HNP (low waterhole density area): 2.1 (±0.1 s.d.) leopards/100 km^2, 1.3 (±1.1) lions/100 km^2, and 6.7 (±1.4) hyaenas/100 km^2 (unpublished data, (Loveridge et al., 2022). Abundance of prey is also higher in the northern part of HNP (e.g. the relative abundance in the north of HNP is ~3 kudu [*Tragelaphus strepsiceros*] records per trap-day and 2 to 5.7 impala [*Aepyceros melampus*] records per trap-day, whereas in the south west of HNP there are ~1 record per trap-day for both kudu and impala) (Sandoval-Serés et al., 2024).

(b) *Camera trap survey*

A total of 487 camera trap stations (two camera traps per station) were deployed during the dry season between 2013 and 2020 across seven surveyed areas within HNP (total effort: 26,030 trap days). Each survey consisted of a mean of 49 (SD ± 14; min 38 to max 78) camera trap stations, and 2527 (SD ± 1133; min 1670 to max 5483) trap days. Camera trap stations were placed on game trails or roads and spaced in a grid of 4 to 5 km apart (Fig. 1; Supporting information, Table S1a).

(c) *Analyses*

Covariates tested

We took the following covariates: season (early dry, late dry), year (2013–2020), vegetation visibility (closed, medium, open), ruggedness of the terrain, Euclidian distance to the closest waterhole, and permanent waterhole densities (number of waterholes within buffer) during the dry season at four different scales (2, 9, 14 km buffer, and per surveyed area). Moreover, we included number of individuals of leopards, lions and hyaenas identified in each camera trap station (small scale), and lion and hyaena densities per the seven surveyed areas (large scale) (Fig. 1). Furthermore, in all models we included trap effort (number of days that a camera trap station was working) (Supporting information, Table S1b).

Low visibility due to dense vegetation and rugged terrain can help wild dogs avoid detection from dominant predators (Davies et al., 2021). We therefore included vegetation visibility and terrain ruggedness as covariates. We attributed a vegetation visibility class to each camera trap station. To do so, we used the vegetation layer (30 m resolution) (Arraut et al., 2018), and categorized grassland and bushed grassland as 'open vegetation', woodland as 'medium vegetation', and bushland and mopane scrub as 'closed vegetation' (Arraut et al., 2018). We calculated terrain ruggedness using the Vector Ruggedness Measure in QGIS 3.12 using a digital elevation layer (~450 m resolution) (NOAA, 2022).

As natural pans highly depend on rainfall to keep having water during the dry season (Chamaillé-Jammes et al., 2007), for each surveyed area, we checked which waterholes (regardless of artificial or natural) had water during the year when the camera trap survey was performed (Fig. 1; Supporting information, Table S1a). To check this, we used data from annual aerial assessments of waterholes with water at the end of the late dry season (WEZ Reports, 2013-2020). To calculate waterhole densities of the dry season (i.e. permanent waterholes), we used four different scales: 2 km radius buffer (as predators prefer to hunt within 2 km of waterholes (Périquet, 2014; Valeix et al., 2010; Van der Meer, 2011), 9 and 14 km radius buffer (as the area under the circle would approximate to the minimum and maximum home range of wild dogs: 260–633 km^2 – [Pomilia et al., 2015]), and per the seven surveyed areas (average area: 2079 km^2; range: 1330 km^2–3712 km^2) (Fig. 1).

The dominant predator densities per surveyed area and per year were taken from Loveridge et al., 2022. Lions were identified through unique whisker spots patterns, leopards and hyaenas were identified through unique pelage patterns, and blurred images were discarded (Loveridge et al., 2022). We checked for collinearity among all covariates with either Pearson or Spearman correlation test (we did not use leopard density as it was correlated to lion density: $r > 0.70$; $p < 0.01$), and we z-standardized all continuous covariates. We performed all our analyses in R (R Core Team, 2023).

Spatial

To answer our question about spatial avoidance (predictions: 1a, 2a, 3a), we fitted a Generalized Linear Mixed Model (GLMM) (family Poisson, log link) (Bolker et al., 2009) with *lme4* package (Bates et al., 2023). We included year ($n = 6$) and survey session ($n = 8$) as random covariates (Fig. 1; Supporting information, Table S1a). We used the number of wild dogs identified per camera trap station as the response variable. We identified wild dogs through unique pelage patterns, and we only took into account the number of wild dogs that were seen on the camera trap regardless of pack size.

Regarding the fixed covariates, we first tested which scale of waterhole density was the best to use in the global model. We then selected a 14 km buffer scale as the model with this scale of waterhole density had the lowest Akaike Information Criterion (AIC). Additionally, to avoid overfitting the global model by including too many covariates and to ensure a good sample size, we tested each environmental covariate separately, and only included in the global model those significant environmental covariates with p-value lower than 0.05 (vegetation visibility). Finally, as we had a good sample size ($n = 366$ observations), we built a global and final model also including the fixed covariates of interest: individuals of leopards, lions and hyaenas per camera trap station (small scale), lion and hyaena densities per surveyed areas (large scale), distance to the closest waterhole and waterhole density within a 14 km buffer. We compared this global model with a null model (the global model had a lower AIC) and performed a goodness-of-fit test of this global model using the pseudo-R^2 (marginal pseudo-R^2 encompasses the variance explained by only the fixed covariates; and conditional pseudo-R^2 encompasses the variance explained by both random and fixed covariates) (Nakagawa and Schielzeth, 2013).

Temporal

To answer our question about temporal avoidance (predictions: 1b, 2b, 3b), we used species activity patterns. First, to assure independence, we excluded those records that were from the same species in the same camera trap station within a period of 1 h (Sample sizes: Supporting information, Table S2) (Niedballa et al., 2019). Then, we estimated the coefficient of overlap Δ (Δ_1 for <75 independent records, and Δ_4 for larger sample sizes) of activity pattern of wild dogs with the other three predators (Meredith and Ridout, 2018; Ridout and Linkie, 2009), and performed 10,000 bootstraps to obtain 95 % confidence intervals using the R package *overlap* (Meredith and Ridout, 2020). To test for statistical differences in the activity pattern of wild dogs and other predators, we calculated the Watson's Two-Sample Test of Homogeneity (Landler et al., 2021) using the R package *circular* (Lund et al., 2017). We classified activity patterns in three different categories: season, area (high waterhole density area located in the North of HNP, against low waterhole density area in the South of HNP: <0.01 waterholes per km^2), and distance to waterholes (close <2 km; medium 2–5 km; far >5 km).

Spatio-temporal (time-to-event models and indices)

To answer our questions about an avoidance response combining both space and time together (predictions: 1ab, 2ab, 3ab), we used time-to-event models and attraction-avoidance ratios (indices). First, we calculated the time difference between different predators detected at each camera trap station within 8-days (large scale) and 1-day (small scale) only for wild dogs with hyaenas (as there was not enough data for wild dogs with leopards and lions).

Then, we fitted time-to-event models (Niedballa et al., 2019; Parsons et al., 2016). We performed Generalized Linear Models (GLMs) (gamma family, log link) using the time difference in hours between a wild dog and a larger predator passing by at the same camera trap station as the dependent variable (using a maximum of 8-days differences for wild dogs with the other three predators, and 1-day differences with wild dogs with hyaenas). In each model, we included number of independent records of wild dogs per camera trap station (to control for differences in wild dogs abundance per site). We also included in each model the order of the species appearing on the camera trap (two options: wild dog appearing first or afterwards). Moreover, to test if any covariate had an effect on the time appearance of wild dogs after a hyaena we fitted GLMs with a subset of the dataset of a hyaena appearing first and then a wild dog (we did not subset data of wild dogs with leopards and lions due to sample size restrictions). We tested the effect of each covariate of interest separately. We selected the models which had covariates with $p < 0.05$. We compared the selected models with a null model (null models had lower AICc than the selected models). We used the McFadden's R^2 as a measure of goodness-of-fit, which encompasses the variance explained by the covariates used (McFadden, 1987). When the models purpose is to explain and not to predict the effect of specific covariates on the outcome, R^2 value is not as crucial for the analyses and can be considered a descriptive and heuristic tool (Hagquist and Stenbeck, 1998; Rafiq et al., 2023).

Additionally to complement the analyses of time-to-event models, we calculated attraction-avoidance ratios using a maximum of 8-days difference (to test a large scale: proactive strategy) for wild dogs with the other three predators and a maximum of 1-day difference (to test a small scale: reactive strategy) only for wild dogs with hyaenas. We calculated the following indices: index AB/BA, and index BAB/BB (Niedballa et al., 2019; Parsons et al., 2016), where: A = other predator, and B = wild dog. We calculated the median of the time intervals of BA (wild dog appears first and then the other predator), AB (other predator appears first and then wild dog), BB (wild dog appearing after a wild dog independent record), and BAB (wild dog appears first, then a predator and then a wild dog again). Values above 1 of both indices indicate non-random movements between the two species (Parsons et al., 2016). We only calculated indices per category (season, area, and distance to waterholes) for wild dogs with hyaenas. All analyses had an adequate sample size of at least 10 records per combination (Supporting information, Table S4) (Niedballa et al., 2019). To compare the observed indices to indices obtained under the null hypothesis, we generated random records per predator (except for wild dogs) (Karanth et al., 2017; Niedballa et al., 2019). While conserving the actual records of wild dogs, we generated 1000 random records of leopards, lions and hyaenas (random times accounting for the diel activity pattern of the predator and random dates within the period of activity of the camera trap in the area). We then compared the observed indices with the indices generated with random records, and calculated the 2.5 % and 97.5 percentile of the random indices distribution.

3. Results

We summarized the main results in Tables 1 and 2.

3.1. Spatial

We found very strong statistical evidence that vegetation visibility (medium vs closed: estimate = −0.66 [SE = 0.20]; $p = 0.001$; open vs closed: estimate = −0.85 [SE = 0.19]; $p < 0.001$; Fig. 2a), number of hyaenas per camera trap station (estimate = 0.067 [SE = 0.011]; $p < 0.001$; Fig. 2c), hyaena density in surveyed areas (estimate = −0.73 [SE = 0.20]; $p < 0.001$; Fig. 2d) were the covariates that were associated with the number of wild dogs identified per camera trap station. Furthermore, we found strong statistical evidence that number of leopards per camera trap station (estimate = 0.16 [SE = 0.07]; $p = 0.01$; Fig. 2b), waterhole distance (estimate = −0.42 [SE = 0.13]; $p = 0.002$; Fig. 2e), and waterhole density within a 14 km buffer (estimate = 0.60 [SE = 0.21]; $p = 0.003$; Fig. 2f) were the covariates that were associated with the number of wild dogs identified per camera trap station (conditional pseudo-$R^2 = 0.57$). There were more wild dogs in areas with closed vegetation visibility (bushland) than in areas with medium and open vegetation visibility (woodland and grassland). There were also more wild dogs with an increase in leopard and hyaena individuals at a camera trap station (small scale), a decrease in hyaena densities (especially above ~14 hyaenas/100 km^2) in surveyed areas (large scale), closer to waterholes and with higher waterhole densities (Fig. 2; Supporting information, Table S4). On the other hand, we did not find statistical evidence that the number of lions in each camera trap station (estimate = −0.01 [SE = 0.027]; $p = 0.81$), nor lion density in the surveyed areas (estimate = 0.57 [SE = 0.47]; $p = 0.23$) had an effect in the wild dog numbers per camera trap station (Supporting information, Table S4). Thus, to recapitulate in the results with regard to spatial avoidance (Table 2), there was no avoidance of wild dogs towards leopards (accept prediction 1a), we did not find an effect of wild dogs avoiding lions (reject prediction 2a). Finally, wild dogs did not avoid hyaenas at a small scale, but avoided hyaenas with a proactive strategy in a large scale (reject prediction 3a).

3.2. Temporal

All predator activity patterns had two main peaks; wild dog activity peaked in crepuscular times (around 06:00 and 18:00); while other predators were more nocturnal with peaks before 06:00 and after 18:00. The wild dog activity pattern did not change with season, waterhole density nor waterhole distance ($p > 0.10$) (Fig. 3; Supporting information, Table S5).

Wild dog activity pattern overlapped the most with leopards (Δ_4 = 0.79 [0.73, 0.86]) and the least with hyaenas activity (Δ_4 = 0.68 [0.63, 0.74]). We found moderate evidence that wild dog activity pattern was different from the other predators ($p < 0.05$); except with leopards in the early dry season, in the high waterhole density area, and in a medium distance from waterholes ($p > 0.10$), where leopards and wild dogs activities overlapped the most (early dry season: Δ_4 = 0.81 [0.69, 0.91]; high waterhole density area: Δ_4 = 0.87 [0.79, 0.93]; medium distance to waterholes: Δ_4 = 0.88 [0.79, 0.95]). Leopard activity pattern changed with seasons and waterhole distribution ($p < 0.01$). In the early dry season and in areas with high waterhole density leopard activity peaks were more crepuscular than nocturnal (more closely resembling wild dogs activity peaks) (Fig. 3; Supporting information, Table S5 and S6).

Wild dog activity overlap with the three other predators' activity was the lowest closer to waterholes (leopards: Δ_1 = 0.67 [0.49, 0.83]; lions: Δ_1 = 0.54 [0.37, 0.70]; hyaenas: Δ_1 = 0.53 [0.37, 0.70]). In these areas close to waterholes, there was hardly any wild dogs activity when dominant predators were the most active (before 06:00 and after 18:00). In contrast, in medium distance to waterholes wild dog activity overlap with lions and hyaenas activity was the highest (lions: Δ_4 = 0.80 [0.69, 0.89]; hyaenas: Δ_4 = 0.78 [0.69, 0.86]); and these differences in the activity overlap of wild dogs with lions and hyaenas between close and medium distance to waterholes were statistically significant (as 95 % confidence intervals did not overlay). On the other hand, we did not find any evidence that wild dog activity overlap with lions and hyaenas activity differed between seasonality and waterhole density (95 % confidence intervals overlapped). However, the tendency was that wild dog activity overlapped more with lion activity in the late dry season (late dry: Δ_4 = 0.73 [0.66, 0.80]; early dry: Δ_4 = 0.67 [0.54, 0.79]) and in the high waterhole density area (high waterhole density: Δ_4 = 0.75 [0.66, 0.83]; low waterhole density: Δ_4 = 0.71 [0.61, 0.80]). Additionally, wild dog activity overlap with hyaenas was almost equal between seasons (Δ = ~0.68), but it was highest in the high waterhole density area (Δ_4 = 0.74 [0.62, 0.88]) and lowest in the low waterhole density area (Δ_4 = 0.62 [0.53, 0.70]) (Fig. 3; Supporting information, Table S7). Hence, to summarize in time (Table 2), there was only avoidance of wild dogs towards leopards in the late dry season, in low waterhole density areas, and close to water (partially accept prediction 1b); and wild dogs proactively avoided lions and hyaenas (accept predictions 2b and 3b).

3.3. Spatio-temporal (time-to-event models and indices)

We did not find any evidence that season, waterhole density or predator density had an effect ($p > 0.14$) on the spatio-temporal dynamics of wild dogs with leopards and lions. However, predator density was the most important one to explain the time difference between wild dogs with leopards and lions. Nor did we find any evidence of attraction or avoidance of wild dogs with leopards and lions ($p > 0.24$). The fact that we did not find any statistical evidence could be due to a small sample size of wild dogs with lions and leopards occurring in the same camera trap station within 8 days (leopards: n = 69; lions: n = 37). This is especially the case for wild dogs and lions (lions and wild dogs appearing on the same location had the smallest sample size), which in itself might indicate that wild dogs avoid lions (Supporting information, Table S3).

When considering a maximum of 1-day difference, hyaenas passed a camera trap station an average ~ 6 h after a wild dog; and wild dogs passed by an estimated average ~ 10 h after a hyaena; and this difference was significant (estimate = −0.47 [SE = 0.21]; $p = 0.03$) (Fig. 4a). However, using a maximum of 8-days difference, there was no evidence of attraction or avoidance of wild dogs with hyaenas (estimate = −0.28 [SE = 0.16]; $p = 0.08$). In a maximum of 1-day difference, there was no effect of any covariates influencing the appearance of a wild dog after a hyaena. In contrast, in a maximum of 8-days difference, wild dogs and

Table 2
Avoidance strategy of African wild dogs towards competing predators.

	Leopard (1)	Lion (2)	Spotted hyaena (3)
Space (a)	No avoidance	No evidence of an effect	No avoidance at small scale. Proactive avoidance at large scale.
Time (b)	Proactive in late dry season, in low waterhole density areas, and close to water.	Proactive (different activity pattern)	Proactive (different activity pattern)
Spatio-temporal (c)	Most likely proactive* but there was not enough data to test	Most likely proactive* but there was not enough data to test	Mainly reactive, (although proactive in the late dry season, closer to water and with lower waterhole densities).

Numbers "1" to "3" and letters "a" to "c" refer to the predictions tested.

[*] Small sample size to test it in a big survey (26,030 trap days; Supporting information, Tables S1, S2 and S3), which in itself most likely indicates avoidance from wild dogs.

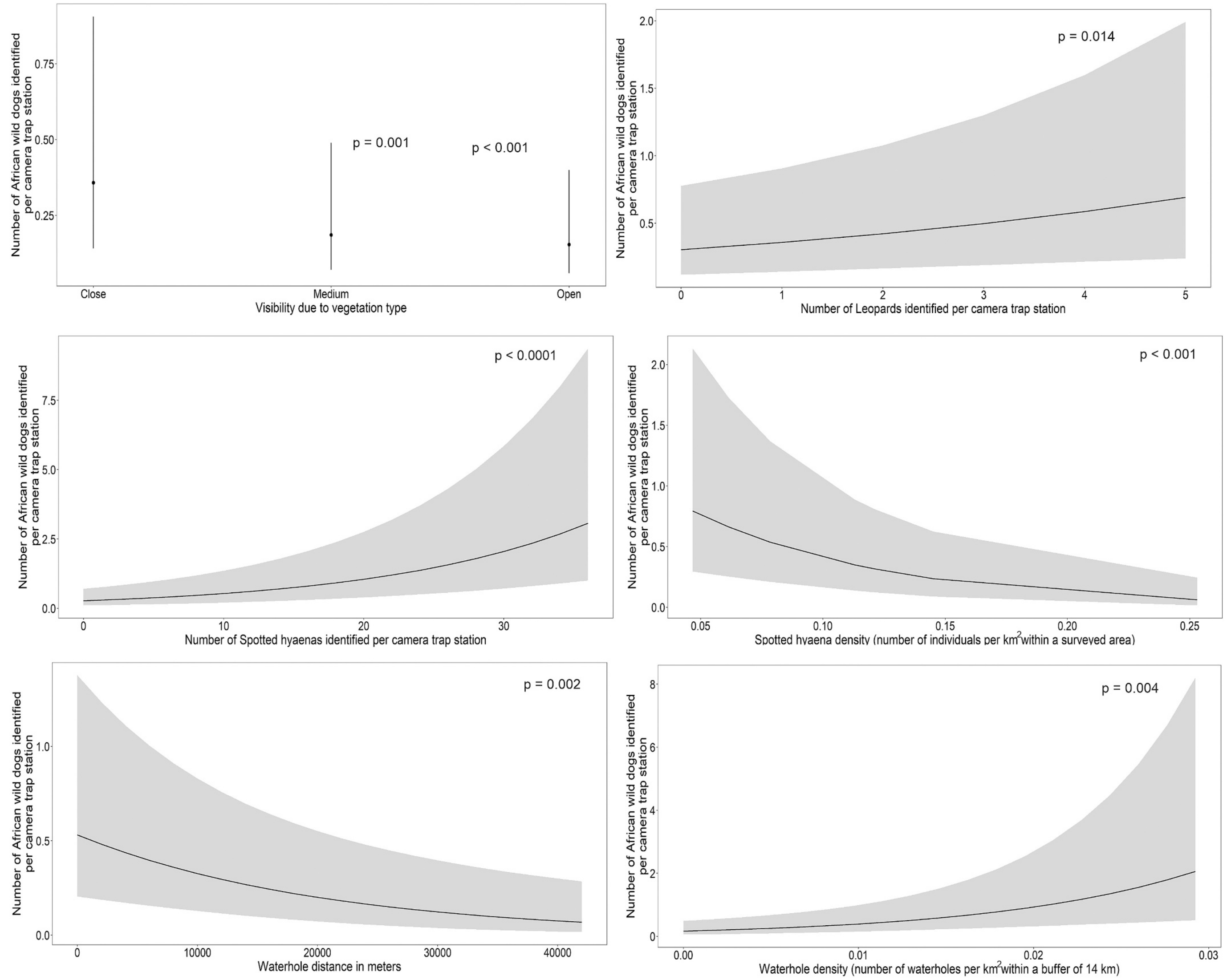


Fig. 2. Results of the spatial model. Marginal back-transformed effects with 95 % confidence intervals of the GLMM of the number of African wild dogs identified per camera trap station per respective covariate (marginal pseudo-R^2 = 0.31; conditional pseudo-R^2 = 0.57). (Supporting information, Table S4).

hyaenas passed closer in time during the early dry season (estimate = −0.48 [SE = 0.18]; p = 0.009) (Fig. 4a). Within 1-day difference, wild dogs took longer to pass after hyaenas when distant from waterholes increased (estimate = −0.35 [SE = 0.16]; p = 0.04), and waterhole density within a buffer of 9 km decreased (estimate = −0.24 [SE = 0.11]; p = 0.02) (Fig. 4b) (Supporting information, Table S7). Regarding the attraction/avoidance indices, all results fell inside the 2.5 % and 97.5 % percentile of the random indices, which indicates that any evidence of wild dog avoidance of predators was not strong (Supporting information, Fig. S1a). Hence, in both space and time (Table 2), we found wild dogs most likely (as we didn't have enough sample size to test) proactively avoided leopards and lions (most likely rejecting, partially, predictions 1ab and most likely accepting predictions 2ab). Finally, wild dogs used a reactive strategy to avoid hyaenas in a small scale and a proactive strategy in a large scale in the late dry season, closer to water and with lower waterhole densities (accept predictions 3ab).

4. Discussion

Avoidance behaviours towards predators (either reactive or proactive) are favoured by subordinate predators when the information about the threat is reliable, the threats fluctuate and when the fitness benefits of avoidance are higher than the costs of encounters (Creel, 2018; Harvell, 1990). Depending on different ecological circumstances the avoidance strategies of subordinate predators can vary spatially and temporarily (Karanth et al., 2017; Vanak et al., 2013; Zhao et al., 2020).

Our main finding was that wild dogs overall used the same space as the other three larger predators, but at different times. When the risk is predictable in time but not space, proactive temporal avoidance is expected and the costs are on the limited time spent in habitat rich in resources (e.g. water and prey) (Palmer et al., 2022). In our study, wild dogs were mainly using a proactive temporal avoidance strategy (different activity pattern) with all three predators. Conversely, when the risk is predictable in space but not in time, proactive spatial avoidance is expected (costs are on the deprivation of prey-rich areas) (Palmer et al., 2022). In our study, when only considering spatial avoidance, wild dogs were not avoiding larger predators at a small scale (same location), and wild dogs were only avoiding hyaenas proactively at a large scale (surveyed area). In addition, although the strength of avoidance of wild dogs towards larger predators was not always strong, we found moderate evidence that wild dogs were using a spatio-temporal proactive avoidance strategy with lions and leopards and a reactive avoidance strategy (same location within 1 day) towards hyaenas. When the risk of

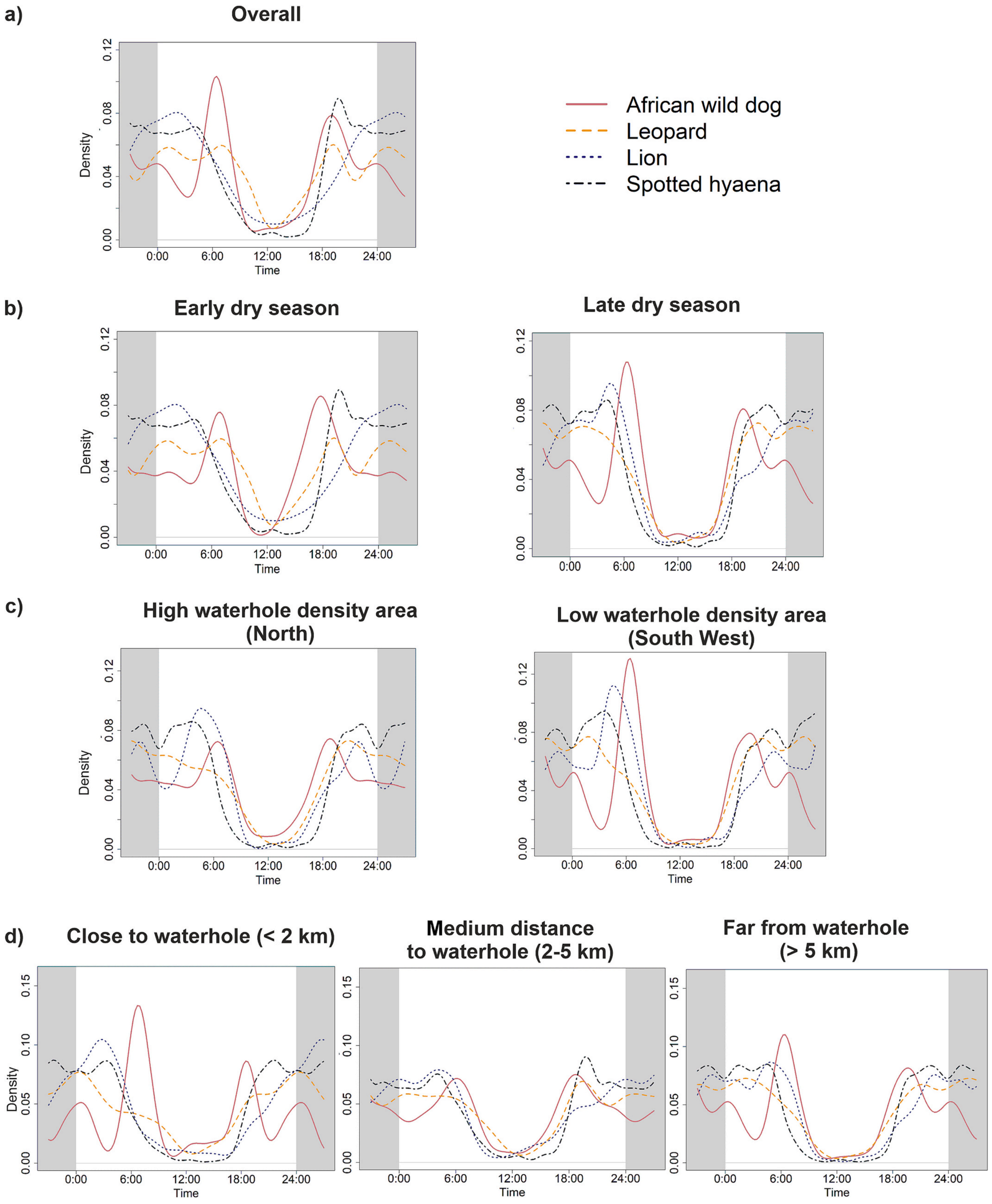
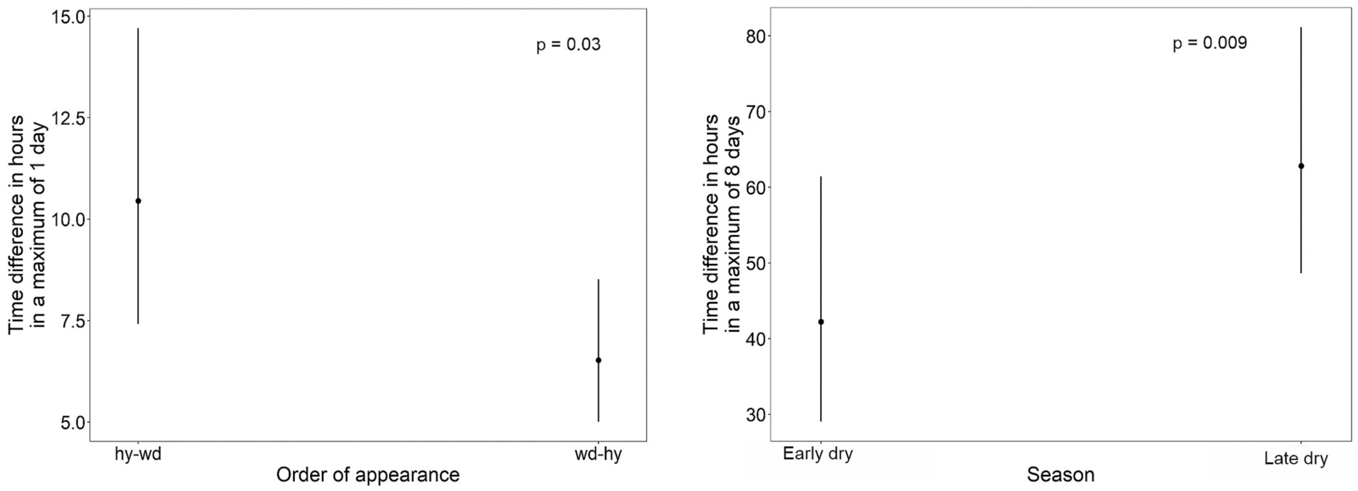


Fig. 3. Activity pattern of African wild dogs and other predators: a) Overall; b) Seasons; c) Areas with different waterhole densities; d) Distance to waterhole. (Supporting information, Tables S6).

a) Time difference between African wild dogs and Spotted hyaenas



b) Time between an African wild dog passing after a Spotted hyaena

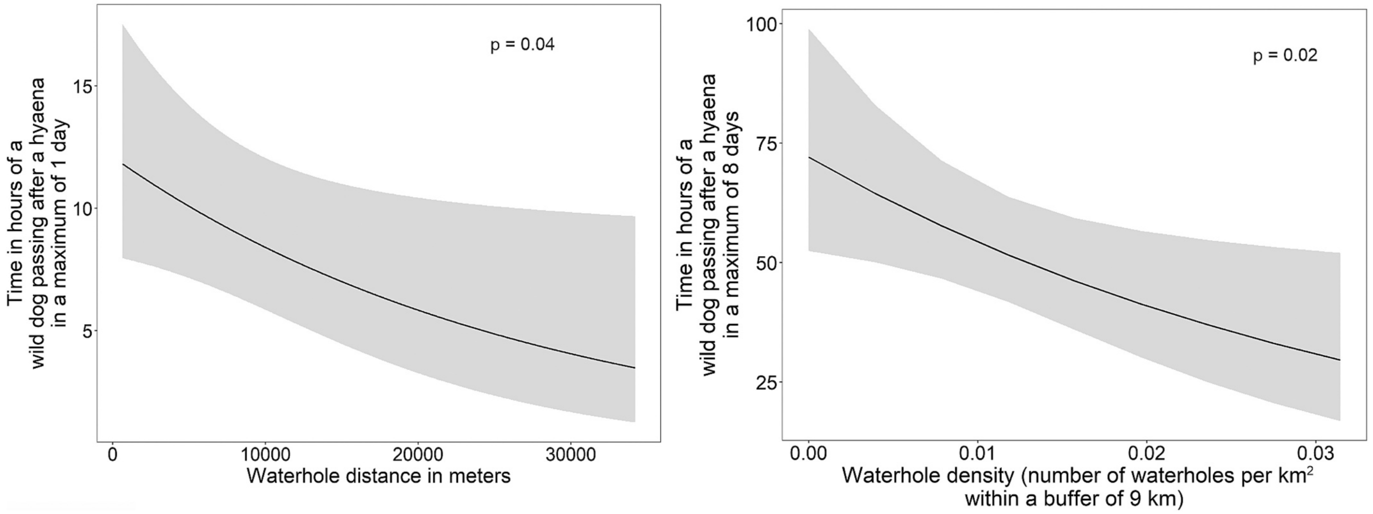


Fig. 4. Marginal effects with 95 % confidence intervals of the best time-to-event analyses of African wild dogs (wd) with Spotted hyaenas (hy). a) Including both order of appearance between wild dogs and hyaenas (in 1-day maximum time: $R^2 = 0.04$; in 8-days maximum time: $R^2 = 0.05$); b) hyaenas appear first then wild dogs (in 1-day maximum time: $R^2 = 0.07$; in 8-days maximum time: $R^2 = 0.06$). (Supporting information, Table S7).

predator encounters is unpredictable in both space and time, then reactive behaviours are expected (Creel, 2018; Palmer et al., 2022).

In various ecosystems, wild dogs actively avoid lions both spatially and temporally at different scales (Darnell et al., 2014; Dröge et al., 2017; Hayward and Slotow, 2009). In our study, wild dogs probably (untested due to a small sample size) avoided lions proactively at a small spatial scale (same location) and time (1 day). This is consistent with most other studies where reactive spatial avoidance behaviours from wild dogs towards lions are less common than proactive behaviours (Davies et al., 2021; Swanson et al., 2014; Vanak et al., 2013). However, Strampelli et al. (2023) found reactive spatial avoidance by wild dogs towards lions at a small-scale (within home range: ~2 km grid); and little evidence of proactive spatial avoidance (at the home range scale: 225 km^2 grid). Conversely, wild dogs do not always exhibit spatial or temporal avoidance towards hyaenas or leopards at different scales (Darnell et al., 2014; Dröge et al., 2017; Strampelli et al., 2023). This could be because the threat hyaenas and leopards pose to wild dogs is not as high as threats posed by lions (Comley et al., 2023; Woodroffe and Ginsberg, 1999). Perhaps, this is why wild dogs did not avoid leopards and hyaenas spatially on a small scale (same location). When spatial avoidance does not occur, subordinate species tend to use temporal avoidance. This aligns with our finding that wild dogs avoided the three predators temporally. Conversely, this can also occur when an increase of temporal overlap is associated to a decrease in spatial overlap (Zhao et al., 2020).

4.1. Influence of covariates

At a large temporal scale, wild dogs were active at different times of the day than lion and hyaenas and to a lesser extent leopard. This temporal proactive avoidance was especially evident close to water with all three competing predators (as expected in our predictions), and with hyaenas and leopards during the late dry season and in low waterhole density areas (contrary to our predictions).

When subordinate species are constrained (e.g. due to resource access restrictions, or periodic increases in competition), they might not be able to strongly avoid the risk of larger predators. Hence, be forced to use a reactive avoidance strategy over a proactive strategy (Darnell et al., 2014; Palmer et al., 2022). In addition, when strong spatial (proactive) avoidance is not possible, wild dogs can implement stronger temporal avoidance instead (Darnell et al., 2014; Palmer et al., 2022). Close to water, wild dogs were using stronger proactive temporal partitioning to avoid the three large predators. Temporal partitioning is commonly seen at waterholes among other African carnivores (Edwards et al., 2015). For instance, in Maremani Reserve (South Africa) wild dogs activity overlapped more with hyaenas at close proximity to waterholes than at roads (Krag et al., 2023). We show the opposite in our study, the highest activity overlap of wild dogs with hyaenas was at medium distances from waterholes. In Maremani Reserve, lions are absent (Krag et al., 2023), thus wild dogs do not need to avoid them temporally at waterholes. This is not the case in HNP, where wild dogs activity overlap with lions was the lowest close to water.

In the late dry season and in the low waterhole density area, wild dogs used a strong avoidance towards hyaenas and leopards. When there is high visibility due to little vegetation to hide during the dry season (in our case late dry season), wild dogs tend to use a stronger avoidance strategy (proactive strategy) towards predators. However, when there is low visibility due to dense vegetation during the wet season (in this case early dry season), wild dogs tend to use a reactive strategy to avoid predators (Vanak et al., 2013). As the risk is difficult to predict (hard to detect potential threats) in low visibility (e.g. early dry season, or closed vegetation), reactive avoidance strategies are favoured. For example, dholes and leopards restrict small-scale avoidance behaviours towards tigers in locations with open vegetation and high visibility (Karanth et al., 2017).

Wild dogs tend to evade dominant predators in space by using habitat structure and altering habitat selection (Davies et al., 2021). In HNP, lions prefer grassland, leopards prefer woodland, and hyaenas prefer both woodland and grassland (Davidson et al., 2012; Loveridge et al., 2022; Périquet, 2014). In our study, we found that wild dogs abundance was higher in closed vegetation (bushland), and lower in medium and open vegetation (woodland and grassland). In dense vegetation, predator encounter risk can be higher due to the risk of ambush (Davies et al., 2021; Webster et al., 2012). However high visibility in open vegetation can also facilitate detection of subordinate species by predators (Janssen et al., 2007), and increase the risk of kleptoparasitism (especially from hyaenas) of wild dog kills (Creel and Creel, 1998). Thus, it appears that wild dogs are dynamic in their habitat use and need landscape heterogeneity to successfully avoid predators (Davies et al., 2021; Dröge et al., 2017; Shumba et al., 2018). Other species also alter their habitat use to avoid dominant predators (e.g. foxes avoiding coyotes - Kozlowski et al., 2011).

Wild dogs in HNP, feed primarily on browsers and mixed feeders, which are prey species found in dense bushland vegetation; and dominant predators select both browsers and grazers, which are found in grassland (Sandoval-Serés et al., 2024). This dietary separation can also enable wild dogs to partition their niche and select habitats where some of their primary prey is found but dominant predators are less likely to occur (e.g. bushland) (Davies et al., 2021; Vanak et al., 2013).

Despite the risk of kleptoparasitism towards wild dogs from hyaenas is lower in low waterhole density areas (Sandoval-Serés et al., in review), wild dogs avoided hyaenas more strongly in the low waterhole density area. This could be because as lions are less abundant in the low waterhole density area, wild dogs had more opportunity to avoid hyaenas in this area because they did not have to strongly avoid lions in the low waterhole density areas.

In our study, and opposite to our predictions, wild dogs used a proactive spatial strategy to avoid hyaenas. In HNP lion densities (~3.5 lions/100km^2) are not as high as in other ecosystems (~12 to 26 lions/100km^2) (Davies et al., 2021; Marneweck et al., 2021), whereas hyaena densities in HNP (~14.1 hyaenas/100 km^2) are not low compared to other ecosystems averaged (~39 hyaenas/100km^2) (Périquet, 2014). Perhaps this explained why wild dogs in our study spatially avoided hyaenas and not lions at a large scale. Moreover, lions and hyaenas tend to aggregate close to waterholes (Davidson et al., 2012; Périquet, 2014; Valeix et al., 2010), and their densities tend to be higher in areas with high waterhole densities (in the north part of HNP) (Loveridge et al., 2022; Sandoval-Serés et al., 2024). Despite this, wild dog abundance in HNP was higher closer to water and in higher waterhole densities. As prey and dominant predators concentrate close to waterholes (Chamaillé-Jammes et al., 2009; Valeix et al., 2010), wild dogs in HNP also tend to hunt close to water (Van der Meer, 2011). Additionally, as prey abundance is higher in the north of HNP where more waterholes are found (Sandoval-Serés et al., 2024), then most likely wild dogs are prioritizing prey encounter over the risk of encountering larger predators. It could be that wild dogs can afford to use the same areas that dominant predators use, because they can hide in dense vegetation and use temporal avoidance, especially when approaching waterholes. Thus, it seems that wild dogs are able to cope with predators as long as there is a heterogeneous landscape (in terms of both waterhole density and vegetation) to be able to hide from larger predators.

Avoiding nutritional-related costs might be the reason why wild dogs in HNP did not normally use a spatial proactive strategy, and preferred to use a temporal strategy to avoid predators instead. As hyaena densities in HNP are higher than the densities of the other larger predators (Cozzi et al., 2013; Loveridge et al., 2022), wild dogs might not be able to spatially avoid hyaenas at small scales, and thus try to avoid them in a large scale (wild dog individuals increasing in areas with less hyaena densities).

4.2. Limitations

In our study, the reactive avoidance behaviours of wild dogs towards competing predators referred to a 24 h scale at the same location. Small-scale spatio-temporal avoidance (<8 days) towards lions and leopards was only inferred indirectly due to small sample sizes. As our data set was large (26,030 trap days) and the sample size was small even in areas with higher abundances of wild dogs and dominant predators, the most probable explanation is that a small sample size indicated that wild dogs actively spatio-temporally avoided lions and leopards at scales of <8 days. Specification of scale is highly important as reactive and proactive strategies can vary depending on the scale used (e.g. it is not the same to use a 2 to 24 h difference than to use a 1 to 8 days difference to test reactive against proactive behaviours).

Finally, we acknowledge the limitation of our analytical approach which does not allow us to account for imperfect species detection. Imperfect detection can sometimes weaken inference in ecological processes; for example, weak species interactions might go undetected (Kellner and Swihart, 2014; Jordano, 2016). We did not find a strong spatio-temporal interaction of wild dogs with lions and leopards which could have potentially been due to a low detection of the three species in camera traps. In Kenya, wild dogs had lower detection probabilities than spotted hyaenas, lions and leopards (Broekhuis et al., 2022). In our global model (GLMM), we included trap effort (days), vegetation visibility (open, medium, close), number of individual lions, hyaenas and leopards, lion and hyaena densities, waterhole distance, and waterhole density (14 buffer). A large sampling effort as well as repeated samples increase the chances of species detection (Jordano, 2016; Royle and Dorazio, 2008; Van der Weyde et al., 2018). A positive aspect of our study is that our data set was large (26,030 trap days) and some surveys were repeated in two different years. Although we did not explicitly account for imperfect detection, we controlled for vegetation visibility and trap effort which could potentially have had an effect on wild dogs' detection. Furthermore, in our global model we included the surveys as a random factor, avoiding pseudo-replication whilst accounting for possible differences among surveys, including survey specific imperfect detection of species. However, factors other than differences among surveyed areas could have also influenced detection probability of species. If detection is imperfect but invariant, the ecological inference might not be weakened (Kellner and Swihart, 2014). Thus, even though we did not test for it, as it was out of the scope of this study, we believe that only if the detection probability of species relative to each other differed significantly could this potentially have affected our inferences. Lastly, it is also important to acknowledge that the individual wild dogs identified per camera trap station should not be interpreted as wild dog density, especially because we did not explicitly account for species detection probability.

4.3. Conservation implications

Spatial and temporal overlap of subordinate predators with dominant predators can increase due to human pressure (Sévêque et al., 2020; Strampelli et al., 2023). Although wild dogs have evolved with larger predators (Turner, 1990), decreased habitats due to anthropogenic factors has provoked that most of large carnivore populations occur within protected areas (Loveridge et al., 2010). Wild dogs select areas at the border of protected areas where they face less competition from lions and hyaenas but higher anthropogenic threats (Van der Meer et al., 2013). It is therefore important to maintain suitable habitat for wild dogs which assists them in coping with dominant predators.

Habitat heterogeneity at different spatial scales is highly important for wild dogs to thrive and to be able to spatially avoid dominant predators (Davies et al., 2021; Dröge et al., 2017). In HNP, wild dogs prefer to use areas with a mixture of different vegetation types (Shumba et al., 2018), which could be due to habitat use alternation and adaptation to avoid larger predators (Davies et al., 2021). In our study, wild dogs were able to coexist in space in the areas with high lion densities (highest lion density: ~6.9 lions/100 km^2 - unpublished data, Loveridge et al., 2022). This was most likely thanks to temporal avoidance and the landscape heterogeneity (probably influenced by waterhole density and distribution) and the availability of dense vegetation. However, wild dogs tend to avoid areas where hyaena densities were too high (especially higher than ~14 hyaenas/100 km^2).

Wild dogs take higher risks to overlap with dominant predators when they need to access critical resources (i.e. water and prey) and when they are not denning (Marneweck et al., 2021; Pretorius et al., 2021; Vanak et al., 2013). As prey is crucial for wild dog survival and reproduction (Creel et al., 2024; Marneweck et al., 2019), encountering prey can outweigh the risk of encountering dominant predators (Cozzi et al., 2012; Creel et al., 2024; Vanak et al., 2013).

We show that very high hyaena densities do not favour wild dogs, especially when there is little water in the system (i.e. in the late dry season and in areas with low waterhole densities). Low water availability can increase food resource competition of wild dogs with lions and hyaenas, and reduce prey abundance (Sandoval-Serés et al., 2024). This can potentially contribute to lower numbers of wild dogs when permanent waterhole densities are too low.

Highly structured habitat and high prey densities are both crucial for wild dogs to thrive and to offset the risks of interspecific competition (Creel et al., 2024; Davies et al., 2021; Marneweck et al., 2021). As waterhole distribution could indirectly have repercussions in the landscape through vegetation changes due to herbivores distribution (Chamaillé-Jammes et al., 2007; Landman et al., 2012), a heterogeneous waterhole distribution could increase landscape heterogeneity and niche-partitioning opportunities (see Morin et al., 2024). In conclusion, we propose a heterogeneous water management provisioning scheme that potentially helps keep enough prey abundance and a heterogeneous landscape. Heterogeneity would also help to increase niche partitioning opportunities to help wild dogs cope better with interspecific competition. This can have further implications in the wide range ecosystems where artificial water provision occurs.

CRediT authorship contribution statement

Elisa Sandoval-Serés: Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Egil Dröge:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **Marion Valeix:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Esther van der Meer:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Lara L. Sousa:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **Justin Seymour-Smith:** Writing – review & editing, Methodology, Data curation. **Andrea Sibanda:** Writing – review & editing, Methodology, Data curation. **Elise Say-Sallaz:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Liz Campbell:** Writing – review & editing, Methodology, Formal analysis. **Duhita Naware:** Writing – review & editing, Methodology, Formal analysis. **Daphine Madhlamoto:** Writing – review & editing, Validation. **Roseline Mandisodza-Chikerema:** Writing – review & editing, Validation. **Andrew J. Loveridge:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

None declared.

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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.2025.111086.

Data availability

The datasets and R code are available in https://figshare.com/, https://doi.org/10.6084/m9.figshare.28607315.v1

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