Interspecific interference competition at the resource patch scale: do large herbivores spatially avoid elephants while accessing water?

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Summary

1. Animals may anticipate and try to avoid, at some costs, physical encounters with other competitors. This may ultimately impact their foraging distribution and intake rates. Such cryptic interference competition is difficult to measure in the field, and extremely little is known at the interspecific level.

2. We tested the hypothesis that smaller species avoid larger ones because of potential costs of interference competition and hence expected them to segregate from larger competitors at the scale of a resource patch. We assessed fine-scale spatial segregation patterns between three African herbivore species (zebra *Equus quagga*, kudu *Tragelaphus strepsiceros* and giraffe *Giraffa camelopardalis*) and a megaherbivore, the African elephant *Loxodonta africana*, at the scale of water resource patches in the semi-arid ecosystem of Hwange National Park, Zimbabwe.

3. Nine waterholes were monitored every two weeks during the dry season of a drought year, and observational scans of the spatial distribution of all herbivores were performed every 15 min. We developed a methodological approach to analyse such fine-scale spatial data.

4. Elephants increasingly used waterholes as the dry season progressed, as did the probability of co-occurrence and agonistic interaction with elephants for the three study species. All three species segregated from elephants at the beginning of the dry season, suggesting a spatial avoidance of elephants and the existence of costs of being close to them. However, contrarily to our expectations, herbivores did not segregate from elephants the rest of the dry season but tended to increasingly aggregate with elephants as the dry season progressed.

5. We discuss these surprising results and the existence of a trade-off between avoidance of interspecific interference competition and other potential factors such as access to quality water, which may have relative associated costs that change with the time of the year.

Key-words: asymmetric interaction, contest competition, distance analysis, *Loxodonta africana*, megaherbivore, savanna, spatial-constrained null model, waterhole use

Introduction

Interspecific interference competition, that is when a species reduces the ability of other species to make use of a shared resource through its presence or agonistic interactions, is ubiquitous in nature (Amarasekare 2002). It has been documented in a wide range of taxa (e.g. Ziv *et al.* (1993) for rodents, Caro & Stoner (2003) for large mammalian carnivores, Elliott (2003) for insects, Razgour, Korine & Saltz (2011) for bats, Colman *et al.* (2012) for large mammalian

herbivores) and can impact individual behaviour (e.g. spatial distribution – Berger & Gese 2007; Broekhuis *et al.* 2013), individual fitness (e.g. Eccard & Ylönen 2002), species coexistence (e.g. Case & Gilpin 1974; Amarasekare 2002) and character displacement (e.g. Grether *et al.* 2009, 2013). In addition to the risk of injury or death during agonistic interactions (e.g. Palomares & Caro 1999; Berger-Tal, Mukherjee & Kotler 2009), interference competition can carry costs that are extremely difficult to evaluate in the field. This is the case when interference competition leads to reduced intake rates (Abramsky, Rosenzweig & Subach 2001) due to apprehension (i.e. attention redirected from

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foraging to predator/competitor detection in a manner that lowers both risk and feeding rate, Kotler, Brown & Dall 2002) or to a reduced access to resources resulting from avoidance behaviour (a process known as cryptic interference competition as such responses are often difficult to observe in the field, Gyimesi, Stillman & Nolet 2010). The need to account for the possibility that animals anticipate and try to avoid, at some costs, physical encounters with other competitors when studying intake rates and foraging distributions has recently been highlighted (Bijleveld, Folmer & Piersma 2012). This may indeed underlie the spatial distribution of animals and their foraging tactics at the community level, and while this has started to be studied at the landscape scale (Vanak & Gompper 2010), and at the inter-patches scale (Razgour, Korine & Saltz 2011), extremely little is known at the finer scale of the resource patch.

Interspecific interactions are often asymmetrical, and smaller species often lose aggressive contests for resources with larger species that are often characterized by stronger traits (e.g. strength, weapons (Peters 1983), see also Durant (2000) for large mammalian carnivores, Cioni & Gherardi (2004) for decapods, Grangier & Lester (2011) for ants and wasps). Therefore, smaller subordinate species are expected to adjust their behaviour to decrease the risk of interference competition with dominant species. Avoidance of dominant competing species can occur at both spatial (Durant 2000; Tannerfeldt, Elmhagen & Angerbjörn 2002) and temporal scales (Ziv *et al.* 1993; Valeix, Chamaillé-Jammes & Fritz 2007). However, overall spatial and temporal avoidance of interference competitors may prevent animals from using very valuable patches of resources. Thus, fine spatio-temporal scale responses should play a crucial role in adjusting the trade-off between avoidance of competitors and access to high-quality resources. This fine-scale spatio-temporal avoidance of interference competition has yet rarely been explored in the field at the interspecific level.

Here, we assessed fine-scale spatial segregation patterns between three African herbivore species and a megaherbivore, the African elephant *Loxodonta africana*, which is expected to dominate all interactions with other herbivores (Owen-Smith 1988), at the scale of a water resource patch. To our knowledge, this intra-patch scale has never been investigated. In arid and semi-arid savannas, surface water resources become scarcer as the dry season progresses and are vital resource patches for water-dependent species survival. This leads to a high level of herbivore aggregation around the remaining water sources at the end of the dry season (Valeix 2011), which can lead to interference behaviour. Behavioural interactions between elephants and other species sometimes lead to other herbivores being chased away from the waterhole area (Valeix, Chamaillé-Jammes & Fritz 2007), and other more extreme interactions can even be the cause of injuries or fatalities, but these are extremely rare (M. Valeix, pers. obs., see also Slotow & van Dyck 2001). Hence, herbivores may anticipate and try to avoid being close to elephants.

Understanding the impact of elephant presence and abundance on other herbivore species at key resource patches, such as waterholes, is crucial in a context where elephant populations have reached high densities in several southern African ecosystems causing concern about their influence on other forms of biodiversity and questioning adequate management options (e.g. Van Aarde & Jackson 2007; Kerley *et al.* 2008). Manipulating surface water distribution has been suggested as an efficient tool to manage high elephant population densities (Chamaillé-Jammes, Valeix & Fritz 2007; Hilbers *et al.* 2015). In this study, we assessed the extent to which cryptic interspecific interference competition between elephants and other herbivores contributes to animal spatial distribution at waterholes and consequently may influence access to water when this resource becomes crucial. The study took place in Hwange National Park, Zimbabwe, an ecosystem characterized by scarce water sources in the dry season (Chamaillé-Jammes, Fritz & Murindagomo 2007a) and one of the largest African elephant populations (Chamaillé-Jammes *et al.* 2008). To assess the fine-scale segregation spatial patterns between elephants and other herbivores, we recorded the distribution of elephants and other herbivores around waterholes, and without previous reference studies, we also developed a methodological approach to analyse such fine-scale spatial data on aggregation/segregation patterns with short term dynamics as well as seasonal changes. We tested the hypothesis that interference competition with elephants is a key driver of herbivore spatial distribution at waterholes and herbivores avoid elephants once at waterholes. We predicted that as the dry season progresses and surface water becomes scarcer, (i) elephants should increasingly use waterholes, (ii) the co-occurrence between elephants and other herbivores at waterholes as well as the frequency of agonistic interactions between them should increase, and (iii) other herbivores should spatially segregate from elephants around waterholes and this pattern should increase throughout the dry season.

Materials and methods

STUDY SITE

The study was carried out in Hwange National Park in the north-western part of Zimbabwe. This ecosystem covers ~15 000 km² of semi-arid dystrophic savanna, mostly on nutrient-poor Kalahari sands. Most rain falls between November and April. The long-term mean annual rainfall is 600 mm but is highly variable (CV ≈ 25%). The study took place during the dry season (i.e. from May until the first rains in October) of a drought year (2003) which received only 474 mm of annual rainfall and followed below average rainfall in 2002 with 363 mm. Hence, the study was carried out under extremely dry conditions. During the dry season, water is only available at artificial waterholes as natural waterholes dry up and appears to be a limiting resource as the increase in the number of artificially pumped waterholes has led to the increase of almost all herbivore

populations (Davison 1967). Animals gather at high densities near waterholes in the dry season (Valeix 2011), and elephants represent 80–90% of the herbivore biomass (Fritz *et al.* 2011). Water depletion at the scale of a waterhole is reduced in the dry season when ground water is actively pumped into water troughs that then fill the artificial waterholes (Appendix S1a, Supporting Information). Thanks to this quasi-permanent renewal of surface water at the end of the dry season, which is the critical period for herbivores in terms of water acquisition, Hwange National Park is an ideal site to study interference mechanisms.

DATA

From May to October 2003, we monitored every two weeks nine artificial waterholes (average diameter of a waterhole: 100 m) during the daytime (from 6 h until 18 h), in the northern part of Hwange National Park (Fig. 1). This represents 1296 h of observation. There were few herbivore observations at these artificial waterholes at the beginning of the dry season, that is in May and June. We pooled data from these 2 months as they were characterized by similar climatic conditions and natural water was still available in the landscape. We thus have five periods (one-2-month and four-1-month) with similar number of observations for the subsequent analyses. During the waterhole monitoring, each herbivore group entering the waterhole area (defined as a ~200-m-radius circle around the waterhole) was recorded (species and group size) as well as all agonistic interactions between elephants and other herbivores (ranging from intimidation with trumpeting to an aggressive chase). Observational scans of the spatial distribution of all herbivores in the waterhole area (scans hereafter) were performed every 15 min in order to describe the spatial distribution of herbivores and ultimately assess the potential for cryptic interference competition. At each scan, the location of animals was recorded on a grid composed of 24 cells

representing the waterhole area (Fig. 2a). For each waterhole, the cells where the water trough was located were recorded. Observations were done from a reasonable distance from the waterhole not to disturb the animals (either from a viewing platform, a tree platform or a vehicle parked at a distance) but not further than 200 m to respect of good visibility condition for observers. The statistical unit considered was the group of individuals of the same species in the same cell (group hereafter). The study focused on the spatial response of three herbivore species to the presence and abundance of elephants: giraffe (*Giraffa camelopardalis* – average body mass = 750 kg), greater kudu (*Tragelaphus strepsiceros* – average body mass = 135 kg) and plains zebra (*Equus quagga* – average body mass = 200 kg). We restricted our analyses to these three species because they were the three only species for which the sample size in co-occurrence with elephants was reasonable for each month and overall allowed for a statistical test of their spatial pattern related to elephant location throughout the dry season. In the dry season, zebra, which is a grazer, is more water dependent than the two other species, which are browsers (Western 1975).

TEMPORAL AND SPATIAL DYNAMICS OF WATERHOLE USE BY ELEPHANTS

Three variables were used to assess the seasonal dynamics of waterhole use by elephants: (i) the number of elephants that visited a waterhole per day, (ii) the percentage of scans with elephants, indicating the amount of time that elephants were present, and (iii) the number of elephants present for each scan, indicating the level of elephant local abundance. We then studied the seasonal dynamics of three other variables describing the spatial use of waterholes by elephants: (i) the number of elephants in the cells 0–8 for each scan, indicating the abundance of elephants potentially drinking or bathing, (ii) the proportion of the cells
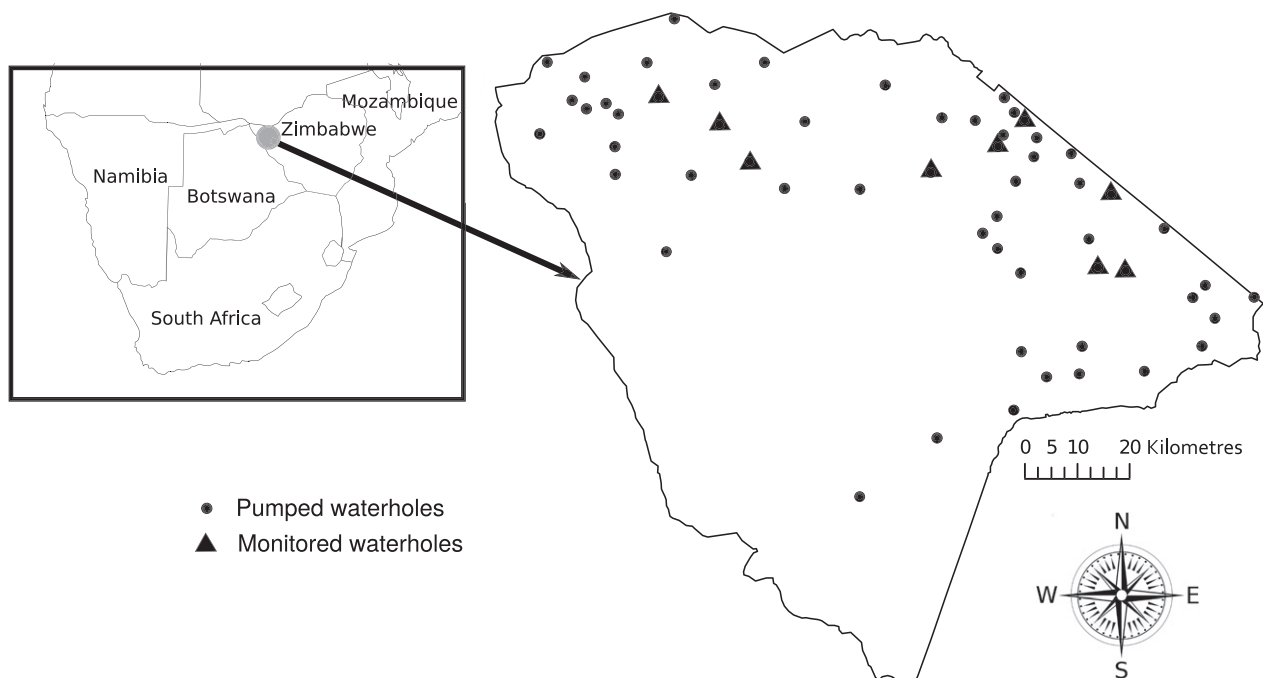
Fig. 1. Map of the distribution of artificial waterholes (dots) in Hwange National Park, Zimbabwe, showing the location of the monitored artificial waterholes (triangles) for this study.

0–24 occupied by elephants, indicating the level of homogeneity in the spatial use of the waterhole area by elephants, and (iii) the proportion of the cells 0–8 occupied by elephants, indicating the level of homogeneity in the spatial use of the water-access area by elephants.

TEMPORAL DYNAMICS OF CO-OCCURRENCE AND INTERACTIONS BETWEEN ELEPHANTS AND HERBIVORES

We investigated the co-occurrence of elephants and other herbivores at waterholes by performing for each study species a logistic regression (dependent variable was 1 for situations of co-occurrence and 0 for situations with no elephant) to test for the increased probability of co-occurrence with elephants at waterholes as the dry season progresses, assuming independence between scans. We then assessed the seasonal dynamics of agonistic behaviours of elephants towards other herbivores by calculating the number of aggressive interactions per month standardized by the number of scans with co-occurrences.

SPATIAL RESPONSE OF HERBIVORES TO WATERHOLE USE BY ELEPHANTS

A least-cost path approach

We considered the distance between a herbivore and an elephant as an inversed proxy of the interaction risk with elephants: the closer the herbivore to an elephant, the riskier the situation in terms of a costly interaction. We modelled the waterhole area using a weighted spatial graph (Dale & Fortin 2010) where each cell corresponds to a node (Fig. 2a). Edges were defined using a queen specification (i.e. polygons that shared common boundaries and vertices) and weighted by the associated Euclidean distances between the centres of cells (Fig. 2b). We then computed distances among nodes (i.e. cells) as the least-cost path on the weighted spatial graph using the Dijsktra's algorithm ('igraph' package for R statistical software 3.3.0, The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). We thus obtained a spatial distance matrix containing the length of least-cost paths for all pairs of cells. For each scan, this distance matrix was used to compute distances between herbivores and elephants. The observed distance of interest in this study and noted D_{obs} is, for scans with one group of the study herbivore species, the distance connecting herbivores to the nearest group of elephants. For scans with several groups of the study herbivore species, we calculated the mean minimum observed distance (D_{obs}) as the average of all groups' minimum observed distance weighted by the number of individuals of each group of herbivores (Fig. 3a). For each scan with co-occurrence between elephants and the other study herbivores, we thus obtained only one value of observed distance (D_{obs}), whatever the number of groups on the scan. This value represented the average behaviour of the study herbivore species in the context of the considered scan.

Spatially constrained null model

The observed intensity of spatial aggregation/segregation for a given scan was evaluated by comparing the statistics D_{obs} to values obtained under the null hypothesis of random distribution of herbivores. We developed a spatially constrained procedure that
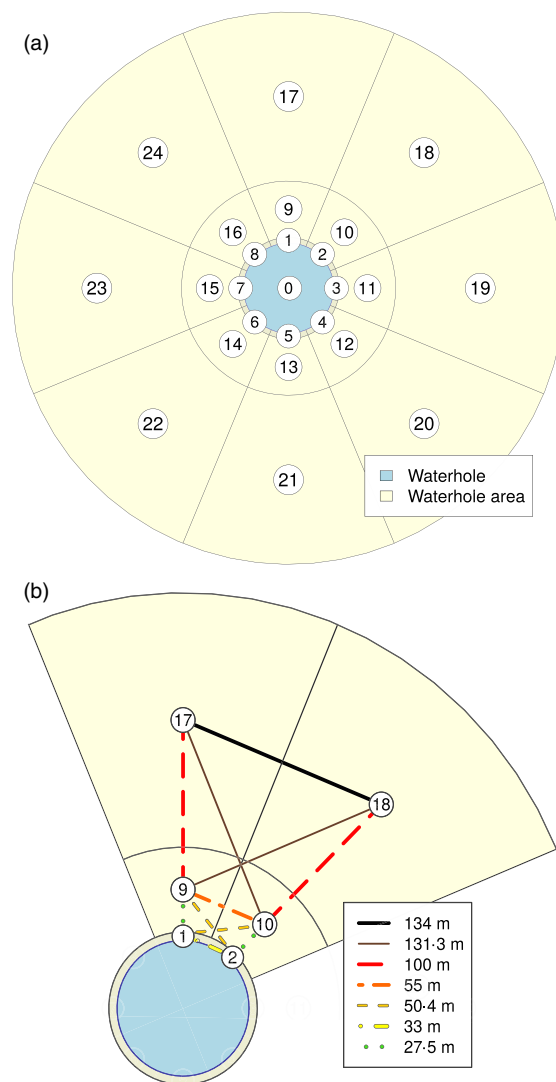
Fig. 2. Spatial sampling design. (a) Representation of the waterhole area divided into four concentric circles: (i) the waterhole itself (cell 0 in pale blue at the centre) where there was most of the time no herbivore except elephants that regularly bath, (ii) the water-access area (cells 1–8, between 0 and 5 m from the waterhole edge) which represents the area where herbivores come into contact with water and can drink, (iii) the intermediate area (cells 9–16, between 5 and 55 m from the waterhole edge) and (iv) the area further away from the waterhole (cells 17–24, between 55 and 205 m from the waterhole edge). For the third and fourth circle, distances were preliminary measured in the field for all study waterholes and specific items in the landscape were used to assess the limits between the different circles of the grid (e.g. a bush, a big hole, a termite mound). (b) Representation of a portion of the weighted spatial graph. Weights were assigned as the distances computed using the average size of the study waterholes.

randomizes the position of the herbivores relative to the elephants but preserves both the locations of elephant groups and the spatial configuration of herbivores (hence the potential for intraspecific interactions) (Fig. 3b). Hence, instead of complete randomization of cells, we rotated and translated the cells occupied by the study herbivore groups but did not modify the spatial distribution of elephants (see Fig. 3c–e for a detailed description
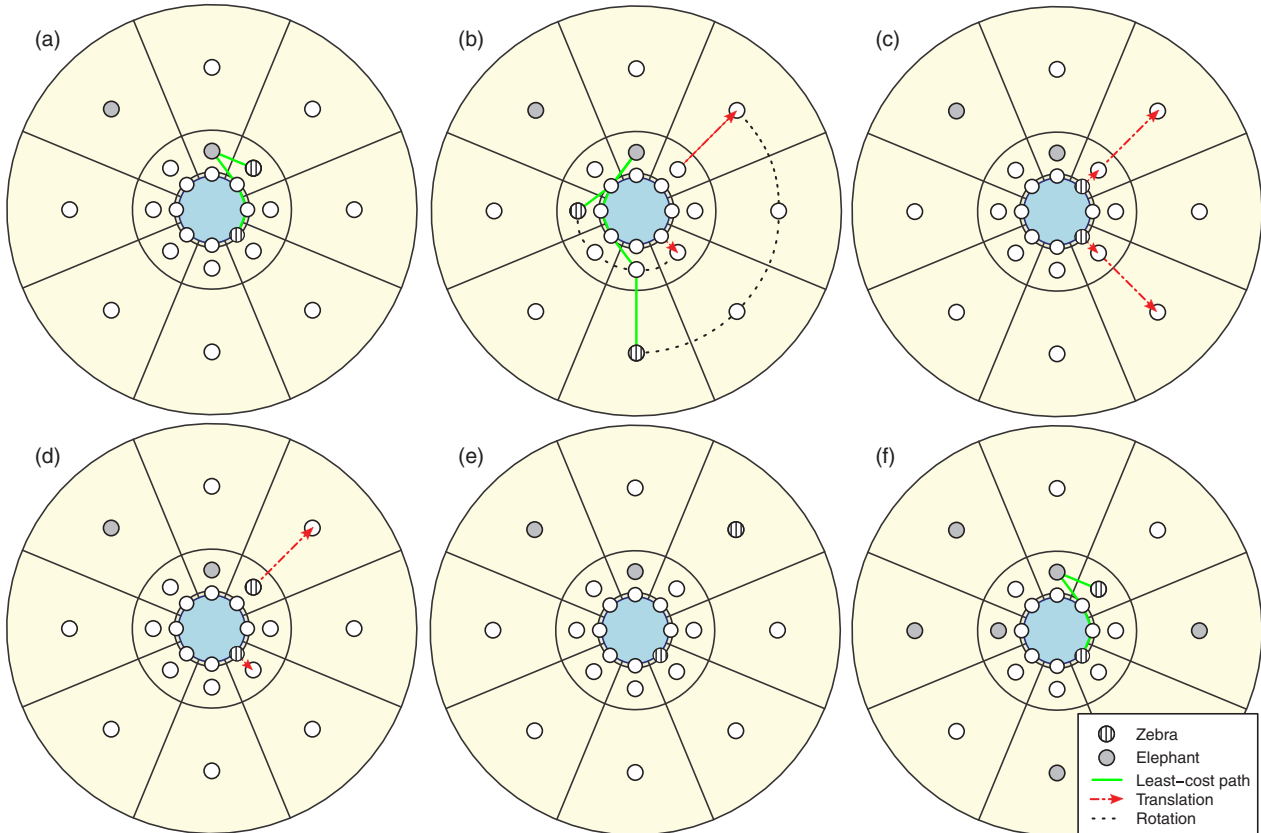
Fig. 3. Illustration of the different steps to calculate the spatial aggregation–segregation index. The occupation of cells is represented as follows : empty cells are white, cells with elephants are grey and cells with zebra are black striped. (a) For each group of the study herbivore species (here zebra), the least-cost path to the closest group of elephants is calculated with the Dijsktra's algorithm (green lines), and the mean of these paths corresponds to the observed distance (D_{obs}) for this scan. (b) For the randomization procedure, we applied a combination of rotations (black arrows) and translations (red arrows) when possible. Green lines represent the new least-cost paths calculated under this randomized scenario. Translations are not always performed in order to preserve the spatial configuration between groups (hence the potential intraspecific interactions). In (c), zebras occupy only one circle, two translations (red arrow) are thus possible without breaking the spatial configuration, whereas in (d), they occupy two circles and only one translation is allowed. If we perform another translation, the spatial configuration of the zebra groups is not respected. Finally, in situation (e) where zebras occupy the two extreme circles, no translation is possible and only eight rotations were then performed. (f) There was a need to take into account the spatial availability in our approach. While in (a) and (f), zebras are at the same distance from a group of elephants, the context is different: in (a), zebras are close to the elephants but have the possibility to occupy a large portion of the waterhole area remaining far enough from the elephants, whereas in (f) they have no other choice than being close to an elephant group, leading to different biological interpretations.

of the procedure). Depending on the observed spatial configuration of herbivores, this randomization procedure can provide up to 24 random values (eight rotations and two translations) and allows to compute the mean ($D_{random_{mean}}$), maximum ($D_{random_{max}}$) and minimum ($D_{random_{min}}$) possible values that could be obtained if herbivores distribute randomly. We repeated this procedure for all scans.

Analysis of spatial aggregation/segregation patterns between herbivores and elephants

To assess variations in aggregation/segregation patterns over the dry season, results were compiled per month (but detailed results for each scan characterized by co-occurrence are provided in Appendix S2). As the range of possible values (defined by $D_{random_{min}}$ and $D_{random_{max}}$) varies between scans, a value of D_{obs} has no meaning per se (compare Fig. 3a and f for an illustration). We thus developed a spatial aggregation/segregation index

(hereafter distance index) that rescales the statistics D_{obs} according to the range of possible values so that it was possible to compare and compile results among scans. Hence, for each scan, we computed:

$$I_{obs} = \frac{|D_{obs} - D_{random_{max}}| - |D_{obs} - D_{random_{min}}|}{|D_{random_{max}} - D_{random_{min}}|},$$

$$I_{random} = \frac{|D_{random_{mean}} - D_{random_{max}}| - |D_{random_{mean}} - D_{random_{min}}|}{|D_{random_{max}} - D_{random_{min}}|}.$$

I_{obs} is the observed distance index whereas I_{random} is the expected value under the null hypothesis for a given scan. The index ranges from -1 (when $D_{obs} = D_{random_{max}}$; i.e. maximal segregation) to 1 (when $D_{obs} = D_{random_{min}}$; i.e. maximal aggregation). Changes in this index over the course of the dry season would indicate a modification of the aggregation/segregation behaviour. For instance, an increased avoidance of elephants by herbivores as the dry season progresses would imply I_{obs} to decrease and

tend to −1 in a more pronounced way than I_{random}. As the response of herbivores can be elephant-density-dependent, we also developed an approach to take into account the average density of elephants around the herbivore group rather than the distance to the closest elephant group (Appendix S3 for details). Results provided by both approaches were similar and thus only results on distance are presented hereafter (Appendix S3 for the results on the impact of the local density of elephants).

Ranks and probability combination test of Stouffer

The statistical significance of the observed segregation/aggregation patterns was evaluated for each month and for each of the three species. For each scan, we determined the rank of the observed distance (D_{obs}) among all random distances (from $D_{random_{min}}$ to $D_{random_{max}}$) computed for the scan. We then calculated a P-value as the probability among these random distances to be equal or superior to the observed distance. Finally, we used the unweighted Z-transform test (Stouffer *et al.* 1949; Whitlock 2005) to combine the P-values obtained in a given month for a given species. As the Fisher's combined probability test, this test allows combining the P-values from k independent tests of the same null hypothesis to calculate a new statistic test that provides 'the significance of the aggregate' of the k independent tests.

Results

TEMPORAL AND SPATIAL DYNAMICS OF WATERHOLE USE BY ELEPHANTS

We observed two phases in the dynamics of elephant use of waterholes. The first phase of the dry season corresponded to a strong increase in the use of waterholes by elephants with the daily number of elephants per waterhole more than tripling between May–June and August, with, respectively (mean ± SE), $126·3 ± 34·6$ elephants and $439·6 ± 137·7$ elephants (Fig. 4a). The second phase of the dry season (between August and October) corresponded to a plateau with a mean of $350 ± 56$ elephants per day at a waterhole, which is significantly higher than during the first phase (KS test = 0·239, $P < 0·05$). Similar patterns were observed for the dynamics of the percentage of scans with elephants with nearly 50% of the scans with elephants between August and October (Fig. 4b, $\chi^2 = 148·85$, $P < 0·001$). Regarding the number of elephants per scan, it started with $17·5 ± 1·3$ elephants per scan in May–June, peaked in August with $31·5 ± 2·0$ elephants per scan and decreased after until $22·4 ± 1·4$ elephants per scan in October (Fig. 4c). Once again the second phase is significantly higher than the first phase concerning the number of elephants per scan (KS test = 0·117, $P < 0·001$). Although there were more elephants per scan as the dry season progressed, the elephant number in the water-access area of waterholes (cells 0–8) did not increase (Fig. 4d). In addition, the proportion of cells occupied, and therefore, the surface area used by elephants, did not increase neither in the entire waterhole area (cells 0–24) nor in the water-access area (cells 0–8) (Fig. 4e,f).

TEMPORAL DYNAMICS OF CO-OCCURRENCE AND INTERACTIONS BETWEEN ELEPHANTS AND HERBIVORES

The probability of co-occurrence with elephants significantly increased over the dry season for the three study species (zebra: $\beta = 0·437$, $P < 0·001$; kudu: $\beta = 0·397$, $P < 0·001$; giraffe: $\beta = 0·278$, $P < 0·001$; see also Fig. 5a–c, respectively). In addition, there was an increase in the percentage of agonistic interactions between elephants and other herbivores reaching almost one-fifth of the scans characterized by co-occurrence between elephants and other herbivores at the end of the dry season (Fig. 5d).

SPATIAL RESPONSE OF HERBIVORES TO WATERHOLE USE BY ELEPHANTS

All three study species tended to segregate from elephants at the beginning of the dry season (see comparison of the median of I_{obs} with the median of I_{random} in Fig. 6), and this pattern was significant for zebras in May–June only (Stouffer test S = 2·95; $P = 0·002$; Fig. 6a). Contrarily to our expectations, herbivores did not segregate from elephants the rest of the dry season but tended to increasingly aggregate with elephants as the dry season progressed (see changes in the median of I_{obs} and changes in the statistics of Stouffer test). This was particularly the case for zebra and kudu for which the median of the observed distance index increased from $I_{obs} = −0·31$ for zebras and $−0·41$ for kudus in May–June to $0·62$ for zebras and $0·60$ for kudus in October (Fig. 6a,b). The distribution of all the observed distance indices with their associated expected value under the null hypothesis of random distribution of herbivores are provided for each month and each study species in Appendix S2. Information on the geographic distance between herbivores and elephants are also provided in Appendix S4.

Discussion

USE OF WATERHOLES BY ELEPHANTS: A HETEROGENEOUS SPATIAL USE OF THE WATERHOLE AREA

In our study, which was during a drought, elephants increasingly used waterholes as the dry season progressed. Not only were elephants more numerous at a given time (higher elephant abundance per scan), but they also used a larger time window (more scans with elephants). The fact that elephants exhibited a larger temporal niche at the end of the dry season corroborates previous findings at the inter-annual scale (Valeix, Chamaillé-Jammes & Fritz 2007), and suggests that elephants, by widening their temporal niche at waterholes, may attempt to avoid intraspecific competition when dry conditions lead to increased elephant abundance. Interestingly, our results
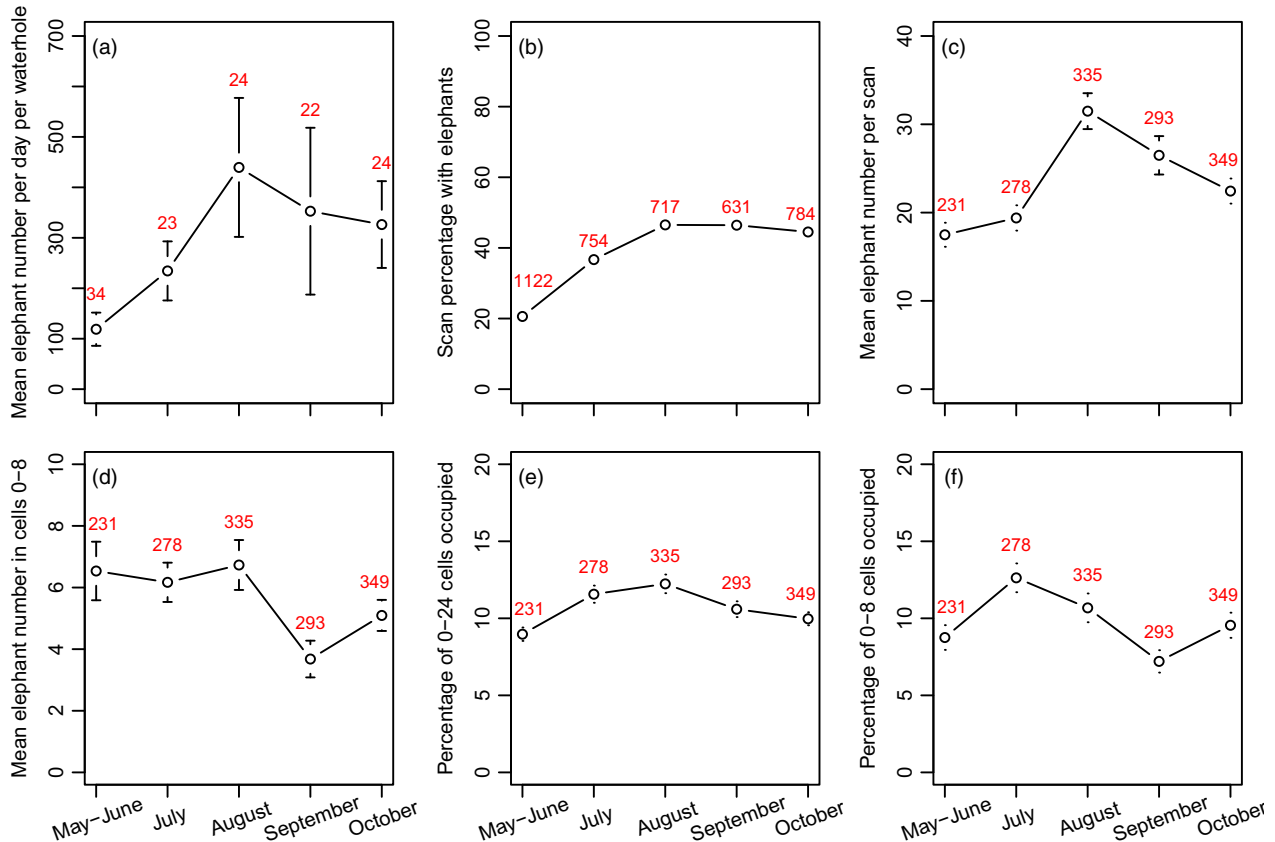
Fig. 4. Dry season dynamics of waterhole use by elephants in Hwange National Park, Zimbabwe, with (a) the mean elephant number (± SE) per day per waterhole, (b) the percentage of scans with elephants, (c) the mean elephant number (± SE) in the waterhole area per scan, (d) the mean elephant number (± SE) in the water-access area (cells 0–8) per scan, (e) the percentage (± SE) of all cells (0–24) occupied by elephants, (f) the percentage (± SE) of cells in the water-access area (0–8) occupied by elephants. Red numbers indicate the number of surveys for (a), the total numbers of scans for (b) and the number of scans with elephants for (c–f).

revealed that this growing number of elephants at waterholes is associated neither with an increase in their use of the entire waterhole area (cells 1–24), nor with an increase in their use of the waterhole access area (cells 1–8), which indicates that elephants aggregate in some specific sectors of the waterhole area. Because animals are expected to be choosier if there is a strong heterogeneity in the resource quality (Sih & Del Giudice 2012), we believe our results could be explained by a strong heterogeneity in the quality of the drinking water between water troughs (where ground water is actively pumped) and the waterhole, and within the waterhole depending on how far animals drink from the area where the pumped water flows from the water trough to the waterhole. Elephants are indeed known to be sensitive to the quality of the water they drink and, for example, seem to be actively looking for sodium-rich water (Weir 1972). Additionally, because of the growing concentration of animals at waterholes, there are significant quantities of faeces, urine and evacuated toxins that accumulate in waterholes as the dry season progresses, leading to higher concentrations of ammonium and a deterioration of the drinking water (F. Hulot, unpublished data). Hence, it is likely that, at the peak of the dry season, elephants are attracted by the

good-quality water available in the water troughs, where clear water is pumped from underground water-table. Alternatively, they would use areas of the waterhole close to where the pumped clear water flows. These preferences would easily explain their aggregation in some sectors of the waterhole area and the fact that they do not use the entire waterhole perimeter (Appendix S1). Some additional results showed that elephants stayed throughout the dry season closer to water troughs than expected under the hypothesis of a random distribution of elephants in the waterhole area (Appendix S5). Consequently, a density-dependent competition phenomenon is likely to occur around water troughs and not at the scale of entire waterhole areas.

SIGNS OF CRYPTIC INTERFERENCE COMPETITION: HERBIVORES SEGREGATE FROM ELEPHANTS AT THE BEGINNING OF THE DRY SEASON

As expected, co-occurrence between elephants and other herbivores, as well as agonistic interactions between them, increased over the course of the dry season, confirming the increased potential for interspecific interference competition between elephants and other herbivores. Our
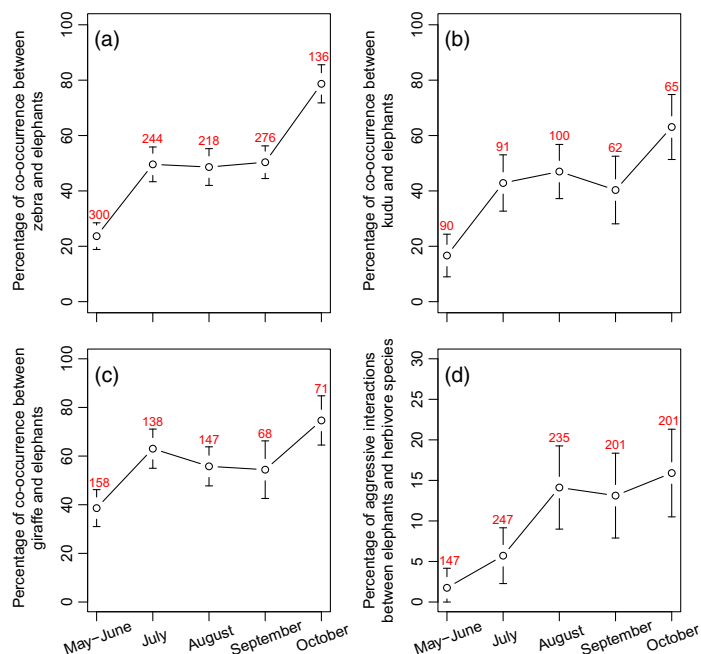
Fig. 5. Dry season dynamics of the percentage of scans with co-occurrence between elephant and (a) zebra, (b) kudu and (c) giraffe at waterholes in Hwange National Park, Zimbabwe. Red numbers for (a), (b) and (c) indicate the total number of scans. (d) Dry season dynamics of the percentage of scans during which there was an aggressive interaction (charge, intimidation, etc.) from elephants against the other herbivores. Red numbers for (d) indicate the number of scans with co-occurrence.

prediction regarding the segregation between other herbivores and elephants during the whole dry season was surprisingly not confirmed as the only significant segregation pattern was in May–June for zebras. However, it is interesting to note that all three study species showed a tendency to segregate from elephants at the beginning of the dry season and that the low sample size for kudus in May–June may have reduced our ability to detect a significant pattern. Hence, herbivores seem to globally segregate from elephants at the beginning of the dry season, suggesting a spatial avoidance of elephants, but not the rest of the dry season. This result does not support a scenario whereby there would be no cost at all of being close to elephants, and provides support for the existence of a moderate cryptic interference competition between elephants and other herbivores. Some potential costs of interference competition with elephants have already been revealed through herbivore temporal niche shifts in dry years to reduce temporal overlap with elephants at waterholes (Valeix, Chamaillé-Jammes & Fritz 2007). Spatial responses to the risk of interference competition with larger competitors have already been revealed at the inter-patch scale (see Razgour, Korine & Saltz (2011) for an example on desert bat communities at waterholes), and our study provides useful insights into how similar mechanisms may occur at the intra-patch scale.

AGGREGATION AT THE END OF THE DRY SEASON: A TRADE-OFF BETWEEN INTERSPECIFIC INTERFERENCE COMPETITION AVOIDANCE AND ACCESS TO QUALITY WATER?

Unexpectedly, herbivores got closer to elephants as the dry season progressed despite the increased level of

potential aggressive interactions from elephants. This was particularly the case for zebras and kudus for which there was a clear tendency to aggregate with elephants in the very dry months. These surprising results are rather counter-intuitive, but we can suggest two possible hypotheses to explain the emergence of these aggregation patterns. First, predation risk is high around water sources in semi-arid savanna ecosystems (Valeix *et al.* 2009a,b; De Boer *et al.* 2010) and is known to strongly influence herbivore behaviour (Lima 1998; Périquet *et al.* 2010). The aggregation of prey whether at the intraspecific level (Lima 1995) or at the interspecific level (Pays, Ekori & Fritz 2014; Schmitt *et al.* 2014) is a widespread anti-predator response to increase detection of predators and a dilution effect. We cannot rule out a scenario whereby herbivores would actively get close to elephants to feel less vulnerable from predators as elephants are rarely attacked by predators and can often chase them away. Unfortunately, this hypothesis could not be explored in this work. Secondly, it is possible that the decrease in water quality in most of the waterhole at the end of the dry season led herbivores to seek the good-quality water found in water troughs and in the waterhole access area where the pumped water arrives. Under this scenario, which is similar for elephants, the herbivores would end up being close to elephants just because both are attracted by the sector around the water troughs, and the observed aggregation patterns would then be a mechanism of passive aggregation. Some additional results are consistent with this hypothesis since we observed an increasing spatial aggregation of herbivores around the water trough over the dry season (Appendix S6). Altogether, our results could suggest the existence of a trade-off between the costs associated with interspecific interference competition highlighted
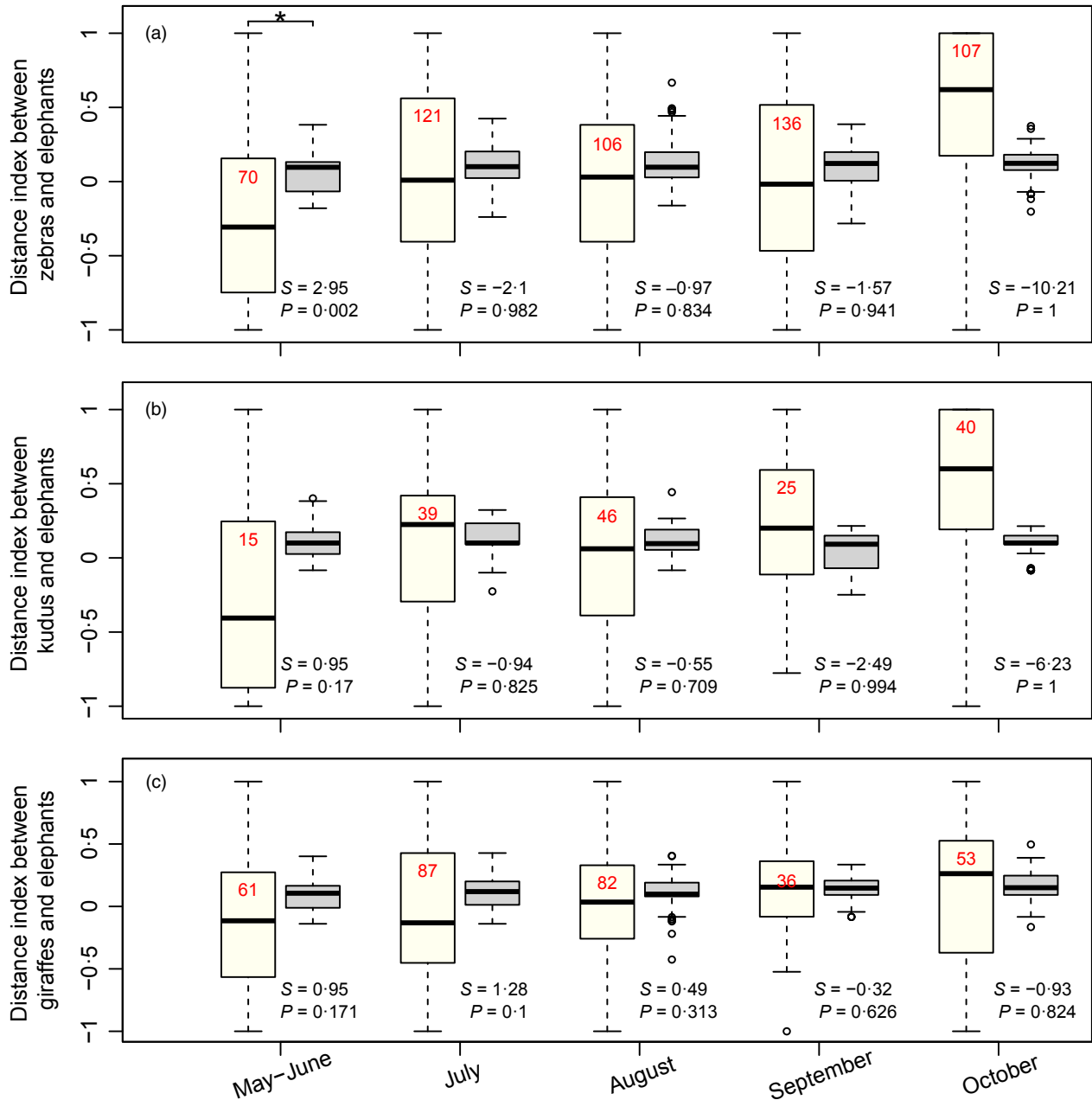
Fig. 6. Dry season dynamics of the spatial aggregation/segregation patterns between herbivores and elephants at waterholes in Hwange National Park, Zimbabwe. White boxplots represent the distribution of the observed distance index I_{obs}. Grey boxplots represent the distribution of the random distance index I_{random} from the null models. Red numbers indicate the number of scans with co-occurrence. S and P-values are the statistics of Stouffer tests for segregation patterns, and stars indicate results which are significant at the P-value of 0·05.

by the avoidance of elephants by herbivores (which seems to be the most important constraint at the beginning of the dry season and explains the segregation patterns) and the costs associated with the access to good-quality water (which seems to be the most important constraint at the end of the dry season). Further, there might be costs associated with waiting for elephants to move away from the clear water since (i) this ultimately decrease the time dedicated to foraging, (ii) there are thermoregulatory costs associated with staying in open areas (see also Valeix,

Chamaillé-Jammes & Fritz 2007), and (iii) it is likely that increased time at waterholes increase herbivore vulnerability to predation as lions are known to ambush their prey around waterholes (Valeix *et al.* 2009b), and further work will be needed to assess their importance.

CONCLUSIONS

The aggregation patterns observed at the end of the dry season could then be explained by the decrease in water

quality over the course of dry season leading to higher costs associated with good-quality water deprivation, which would ultimately exceed those associated to interference competition with elephants. While herbivores can afford to avoid elephants at the beginning of the dry season, which clearly indicates that there are some potential costs associated to interspecific interference competition with elephants, they have no choice than being close to them at the end of the dry season to access some good-quality drinking water. This study illustrates the importance of studying interference phenomena over large temporal windows as the shift in segregation/aggregation patterns over the course of the dry season allowed us to identify this possible trade-off. To our knowledge, our work is one of the first studies to highlight such trade-off in the field. The logical next step to this study is to determine the impact of both avoidance of interference and good-quality water deficiency in terms of physiological/energetic costs in order to quantify the costs of interference competition (e.g. Abramsky, Rosenzweig & Subach (2001) in laboratory). Our results also encourage for further studies on the heterogeneity of water quality in water sources and on the associated implications in terms of attractiveness for wildlife. It paves the way for a reflection on the impact of water trough design on wildlife (see also Pinheiro Machado Filho *et al.* (2004) for livestock).

This study also seems to suggest that different ecological constraints lead to different trade-offs between avoidance of interference competition and access to good-quality water. Indeed, giraffe is the only species that did not get close to elephants and appeared to maintain a minimum distance from elephants. Our results also revealed that they tended to avoid areas of the waterhole characterized by high surrounding elephant abundances. This is consistent with the fact that giraffe is the only of the three study species to react negatively to the abundance of elephants for the probability of drinking once at a waterhole (Valeix *et al.* 2008a). This may be explained by the fact that giraffes are known to be less water dependent than the two other species (Western 1975) and could thus afford to wait for longer periods before accessing water. Moreover, drinking is the only activity when giraffes are vulnerable to costly interactions such as predation or interference competition because of their splay-legged posture. Our results further revealed a high variability in the fine-scale spatial responses at the population level for the three study species, illustrating high group variability (Appendix S2). Some individuals are more risk-prone than others depending on their body condition (Mikolajewski, Johansson & Brodin 2004), physiology (Leary *et al.* 2004) or personality (Quinn *et al.* 2012), and this may influence group decision. This also constitutes an important field of investigation for future research.

Ultimately, our work provides useful information into the impact of high elephant population densities on other herbivores, particularly in the context of increasing frequency and magnitude of droughts (Holmgren *et al.* 2006;

Chamaillé-Jammes, Fritz & Murindagomo 2007b) as the frequency and strength of interspecific interactions at water sources are expected to increase. Understanding the impact of these interactions on the functioning of animal communities is important to improve conservation and management policies (Van der Putten, Macel & Visser 2010). This is especially true in Hwange National Park, which has been characterized by a strong increase in elephant densities (Chamaillé-Jammes *et al.* 2008) and where most of the other herbivore species have shown declines in their populations (Valeix *et al.* 2008b) rising concerns about the impact of elephants on other herbivore species. Our work shows that while there seem to be some costs associated to cryptic interference competition with elephants, these costs are not high enough to prevent other herbivores from accessing high-quality resources at the peak of the dry season when water requirements are crucial. Our work provides an original contribution by pointing out the potential importance of water troughs and water quality provisioning. We hope this will be useful for a better understanding of the role of the interaction between elephants and water in the functioning of herbivore communities and savanna ecosystems and ultimately a better designing of surface water management plans in arid and semi-arid ecosystems (Smit, Grant & Devereux 2007; Hilbers *et al.* 2015).

Data accessibility

Data available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.1f663 (Ferry *et al.* 2016).

References

Abramsky, Z., Rosenzweig, M.L. & Subach, A. (2001) The cost of interspecific competition in two gerbil species. *Journal of Animal Ecology*, **70**, 561–567.

Amarasekare, P. (2002) Interference competition and species coexistence. *Proceedings of The Royal Society B: Biological Sciences*, **269**, 2541–2550.

Berger, K.M. & Gese, E.M. (2007) Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology*, **76**, 1075–1085.

Berger-Tal, O., Mukherjee, S. & Kotler, B.P. (2009) Look before you leap: is risk of injury a foraging cost? *Behavioral Ecology and Sociobiology*, **63**, 1821–1827.

Bijleveld, A.I., Folmer, E.O. & Piersma, T. (2012) Experimental evidence for cryptic interference among socially foraging shorebirds. *Behavioral Ecology*, **23**, 806–814.

Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J.W. & Macdonald, D.W. (2013) Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology*, **82**, 1098–1105.

Caro, T.M. & Stoner, C.J. (2003) The potential for interspecific competition among African carnivores. *Biological Conservation*, **110**, 67–75.

Case, T.M. & Gilpin, M. (1974) Interference competition and niche theory. *Proceedings of the National Academy of Sciences of the United States of America*, **71**, 3073–3077.

Chamaillé-Jammes, S., Fritz, H. & Murindagomo, F. (2007a) Climate-driven fluctuations in surface-water availability and the buffering role of artificial pumping in an African savanna: potential implication for herbivore dynamics. *Diversity and Distributions*, **13**, 663–665.

Chamaillé-Jammes, S., Fritz, H. & Murindagomo, F. (2007b) Detecting climate changes of concern in highly variable environments: quantile regressions reveal that droughts worsen in Hwange National Park, Zimbabwe. *Journal of Arid Environments*, **71**, 321–326.

Chamaillé-Jammes, S., Valeix, M. & Fritz, H. (2007) Managing heterogeneity in elephant distribution: interactions between elephant population density and surface water availability. *Journal of Applied Ecology*, **44**, 625–633.

Chamaillé-Jammes, S., Fritz, H., Valeix, M., Murindagomo, F. & Clobert, J. (2008) Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. *Journal of Animal Ecology*, **77**, 135–144.

Cioni, A. & Gherardi, F. (2004) Agonism and interference competition in freshwater decapods. *Behaviour*, **141**, 1297–1324.

Colman, J.E., Tsegaye, D., Pedersen, C., Eidesen, R., Arntsen, H., Holand, Ø. et al. (2012) Behavioral interference between sympatric reindeer and domesticated sheep in Norway. *Rangeland Ecology & Management*, **65**, 299–308.

Dale, M.R.T. & Fortin, M.-J. (2010) From graphs to spatial graphs. *Annual Review of Ecology Evolution and Systematics*, **41**, 21–38.

Davidson, Z., Valeix, M., van Kesteren, F., Loveridge, A.J., Hunt, J.E., Murindagomo, F. et al. (2013) Seasonal diet and prey preference of the African lion in waterhole-driven semi-arid savanna. *PLoS One*, **8**, e55182.

Davison, T. (1967) *Wankie: the Story of a Great Game Reserve*. Thorntree Press, Bulawayo, Zimbabwe.

De Boer, W.F., Vis, M.J.P., de Knegt, H.J., Rowles, C., Kohl, E.M., van Langeveld, F. et al. (2010) Spatial distribution of lion kills determined by the water dependency of prey-species. *Journal of Mammalogy*, **91**, 1280–1286.

Durant, S.M. (2000) Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, **11**, 624–632.

Eccard, J.A. & Ylönen, H. (2002) Direct interference or indirect exploitation? An experimental study of fitness costs of interspecific competition in voles. *Oikos*, **99**, 580–590.

Elliott, J.M. (2003) Interspecific interference and the functional response of four species of carnivorous stoneflies. *Freshwater Biology*, **48**, 1527–1539.

Ferry, N., Dray, S., Fritz, H. & Valeix, M. (2016) Data from: Interspecific interference competition at the resource patch scale: do large herbivores spatially avoid elephants while accessing water? *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.1f663.

Fritz, H., Loreau, M., Chamaillé-Jammes, S., Valeix, M. & Clobert, J. (2011) A food web perspective on large herbivore community limitation. *Ecography*, **34**, 196–202.

Grangier, J. & Lester, P. (2011) A novel interference behaviour: invasive wasps remove ants from resources and drop them from a height. *Biology Letters*, **7**, 664–667.

Grether, G.F., Losin, N., Anderson, C.N. & Okamoto, K. (2009) The role of interspecific interference competition in character displacement and the evolution of competitor recognition. *Biological Reviews*, **84**, 617–635.

Grether, G.F., Anderson, C.N., Drury, J.P., Kirschel, A.N.G., Losin, N., Okamoto, K. et al. (2013) The evolutionary consequences of interspecific aggression. *Annals of the New York Academy Sciences*, **1289**, 48–68.

Gyimesi, A., Stillman, R.A. & Nolet, B.A. (2010) Cryptic interference competition in swans foraging on cryptic prey. *Animal Behaviour*, **80**, 791–797.

Hilbers, J.P., van Langevelde, F., Prins, H.H., Grant, C.C., Peel, M.J., Coughenour, M.B. et al. (2015) Modeling elephant-mediated cascading effects of water point closure. *Ecological Applications*, **25**, 402–415.

Holmgren, M., Stapp, P., Dicjman, C.R., Gracia, C., Graham, S., Gutiérrez, J.R. et al. (2006) Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment*, **4**, 87–95.

Kerley, G.I.H., Landman, M., Kruger, L., Owen-Smith, N., Balfour, D., de Boer, W. et al. (2008) Effects of elephants on ecosystems and biodiversity. *Elephant Management: A Scientific Assessment of South Africa* (eds R.J. Scholes & K. Mennell), pp. 146–205. Wits University Press, Johannesburg, South Africa.

Kotler, B.P., Brown, J.S. & Dall, S.R.X. (2002) Foraging games between owls and gerbils: temporal dynamics of resource depletion and apprehension in gerbils. *Evolutionary Ecology Research*, **4**, 495–518.

Leary, C.J., Jessop, T.S., Garcia, A.M. & Knapp, R. (2004) Steroid hormone profiles and relative body condition of calling and satellite toads: implications for proximate regulation of behavior in anurans. *Behavioral Ecology*, **15**, 313–320.

Lima, S.L. (1995) Back to the basics of anti-predatory vigilance: the group size effect. *Animal Behaviour*, **49**, 11–20.

Lima, S.L. (1998) Nonlethal effects in the ecology of predator-prey interactions. *BioScience*, **48**, 25–34.

Mikolajewski, D.J., Johansson, F. & Brodin, T. (2004) Condition-dependent behaviour among damselfly populations. *Canadian Journal of Zoology*, **82**, 653–659.

Owen-Smith, R.N. (1988) *Megaherbivores: the Influence of Very Large Body Size on Ecology*. Cambridge University Press, Cambridge, UK.

Palomares, F. & Caro, T.M. (1999) Interspecific killing among mammalian carnivores. *American Society of Naturalists*, **153**, 492–508.

Pays, O., Ekori, A. & Fritz, H. (2014) On the advantages of mixed-species groups: impalas adjust their vigilance when associated with larger prey herbivores. *Ethology*, **120**, 1207–1216.

Périquet, S., Valeix, M., Loveridge, A.J., Madzikanda, H., Macdonald, D.W. & Fritz, H. (2010) Individual vigilance of African herbivores while drinking: the role of immediate predation and context. *Animal Behaviour*, **79**, 665–671.

Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, UK.

Pinheiro Machado Filho, L.C., Teixeira, D.L., Weary, D.M., von Keyserlingk, M.A.G. & Hötzel, M.J. (2004) Designing better water troughs: dairy cows prefer and drink more from larger troughs. *Applied Animal Behaviour Science*, **89**, 185–193.

Quinn, J.L., Cole, E.F., Bates, J., Payne, R.W. & Cresswell, W. (2012) Personality predicts individual responsiveness to the risks of starvation and predation. *Proceedings of the Royal Society B*, **279**, 1919–1926.

Razgour, O., Korine, C. & Saltz, D. (2011) Does interspecific competition drive patterns of habitat use in desert bat communities? *Oecologia*, **167**, 493–502.

Schmitt, M.H., Stears, K., Wilmers, C.C. & Shrader, A.M. (2014) Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds. *Animal Behaviour*, **96**, 151–158.

Sih, A. & Del Giudice, M. (2012) Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philosophical Transactions of the Royal Society B*, **367**, 2762–2772.

Slotow, R. & van Dyck, G. (2001) Role of delinquent young "orphan" male elephants in high mortality of white rhinoceros in Pilanesberg National Park, South Africa. *Koedoe*, **44**, 85–94.

Smit, I., Grant, C.C. & Devereux, B.J. (2007) Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, **136**, 85–99.

Stouffer, S.A., Suchman, E.A., DeVinney, L.C., Star, S.A. & Williams, R.M. Jr. (1949) *The American Soldier, Vol. 1: Adjustments During Army Life*. Princeton University Press, Princeton, NJ, USA.

Tannerfeldt, M., Elmhagen, B. & Angerbjörn, A. (2002) Exclusion by interference competition? The relationship between red and artic foxes. *Oecologia*, **132**, 213–220.

Valeix, M. (2011) Temporal dynamics of dry-season water-hole use by large African herbivores in two years of contrasting rainfall in Hwange National Park, Zimbabwe. *Journal of Tropical Ecology*, **27**, 163–170.

Valeix, M., Chamaillé-Jammes, S. & Fritz, H. (2007) Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. *Oecologia*, **153**, 739–748.

Valeix, M., Fritz, H., Matsika, R., Matsvimbo, F. & Madzikanda, H. (2008a) The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. *African Journal of Ecology*, **46**, 402–410.

Valeix, M., Fritz, H., Chamaillé-Jammes, S., Bourgarel, M. & Murindagomo, F. (2008b) Fluctuations in abundance of large herbivore populations: insights into the influence of dry season rainfall and elephant numbers from long-term data. *Animal Conservation*, **11**, 391–400.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. *et al.* (2009a) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, **90**, 23–30.

Valeix, M., Fritz, H., Loveridge, A.J., Davidson, Z., Hunt, J.E., Murindagomo, F. *et al.* (2009b) Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioral Ecology and Sociobiology*, **63**, 1483–1494.

Valeix, M., Loveridge, A.J., Davidson, Z., Madzikanda, H., Fritz, H. & Macdonald, D.W. (2010) How key habitat features influences large terrestrial carnivore movements: waterholes and African lions in a semiarid savanna of north-western Zimbabwe. *Landscape Ecology*, **25**, 337–351.

Van Aarde, R.J. & Jackson, T.P. (2007) Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. *Biological Conservation*, **134**, 289–297.

Van der Putten, W.H., Macel, M. & Visser, M.E. (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B*, **365**, 2025–2034.

Vanak, A.T. & Gompper, M.E. (2010) Interference competition at the landscape level: the effect of free-ranging dogs on a native mesocarnivore. *Journal of Applied Ecology*, **47**, 1225–1232.

Weir, J.S. (1972) Spatial distribution of elephants in an African National Park in relation to environmental sodium. *Oikos*, **23**, 1–13.

Western, D. (1975) Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal*, **13**, 265–286.

Whitlock, M.C. (2005) Combining probability from independent tests: the weighted Z-method is superior to Fisher's approach. *Journal of Evolutionary Biology*, **18**, 1368–1373.

Ziv, Y., Abramsky, Z., Kotler, B.P. & Subach, A. (1993) Interference competition and temporal and habitat partitioning in two gerbil species. *Oikos*, **66**, 237–246.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. (a) Elephants drinking at a water-trough. The pumped water is then directed to the waterhole. (b) Elephant aggregation around a water-trough area.

Appendix S2. Distribution of the observed distance index with their associated expected value under the null hypothesis of random distribution of herbivores for each month and each study species.

Appendix S3. Analysis of the spatial response of herbivores to the surrounding elephant local abundance.

Appendix S4. Distances (in m) between elephants and other herbivores throughout the dry season.

Appendix S5. Analyses of the spatial relationship between elephants and water-troughs in Hwange National Park, Zimbabwe.

Appendix S6. Dry season dynamics of the distance between herbivore groups and water-troughs.