Do elephants prevent other African herbivores from using waterholes in the dry season?

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Abstract In some African protected areas, concerns have arisen about the influence of locally high elephant numbers on other forms of biodiversity. In arid and semi-arid savannas, surface-water resources are scarce and agonistic interactions between elephants and other herbivores have been reported at waterholes, yet surprisingly very little is known about the impact of elephants on the use of waterholes by other herbivores. Here, we test whether when there are elephants at a waterhole, other herbivores (1) do not change their drinking behaviour; (2) spend shorter time around the water because they are disturbed by elephants' presence and consequently have to leave the waterhole area probably without having met their water requirements, or (3) spend more time around the water probably owing to an increase in vigilance activities or because the presence of elephants may signal safety from predators. Results show that all species spend longer time around water when

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there are elephants at the waterhole, although the difference is not large. Consequently, this study strongly suggests that elephants do not prevent other herbivores from drinking (time at waterholes is not shortened when elephants are around). Further, if the additional time spent to drink is linked to an increased vigilance, the difference is not large, and hence unlikely to affect the population dynamics of other herbivores.

Introduction

In African arid and semi-arid savannas, surface water resources dry up or become depleted as the dry season progresses, resulting in scarcity and, consequently, in strong constraints for animals. Wildlife managers have always been concerned by animal die-offs that can be caused by drought in such ecosystems (Dunham 1994; Young 1994; Dudley et al. 2001), and water provision has ranked as one of the main management interventions in African protected areas and game ranches (Owen-Smith 1996). What happens at waterholes in dry years (e.g. competition) may be crucial in understanding herbivore community functioning. Unfortunately, if high levels of animal aggregations have been reported at waterholes (Thrash et al. 1995), extremely little is known on the behavioural consequences of such aggregations.

Thanks to the creation of waterholes in some areas, and also to efficient anti-poaching efforts, elephant populations have strongly increased over the past decades in southern Africa (Blanc et al. 2005) and some countries now face problems linked to overabundance of elephants. These problems are worsened by the compression of the ranges of elephant populations due to human extension (Parker and Graham 1989). Consequently, concerns have arisen about the influence of locally high elephant numbers on their ecosystem and other forms of biodiversity. If many studies have focused on the impact of elephants on vegetation (review in Conybeare 2004), fewer studies have focused on the consequences of elephant-induced vegetation changes on other animals (Herremans 1995; Cumming et al. 1997; Fenton et al. 1998; Rutina et al. 2005; Makhabu et al. 2006; Pringle 2008). Besides, even though agonistic interactions between elephants and other herbivores have been reported at waterholes (Berger and Cunningham 1998; Valeix et al. 2007a), little is known about the impact of elephants on the use of waterholes by other herbivores (but see Valeix et al. 2007a, b). In addition to an understanding of the relationship between surface-water and herbivore populations (e.g. Redfern et al. 2003; Chamaillé-Jammes et al. 2007), successful managment of African savanna ecosystems will therefore requires an understanding of the behavioural consequences of herbivore aggregation at waterholes, and particularly of the effects of elephants on sympatric large herbivore species.

Interference phenomena resulting from aggregative response have been mainly studied in the framework of foraging behaviour (e.g. Fryxell 1991; Rowcliffe et al. 1999), and many field studies have shown that when competitor density is high, some individuals tend to monopolise resources and subordinate individuals spend more time in vigilance activities, which leads to reduced food intake rate and potentially to a reduced quantity of ingested resources (Ens and Goss-Custard 1984; Dolman 1995; Cresswell 1998). In this study, we tested three possible effects induced by the presence of potential keystone competitors (sensu Bond 1993), such as African elephants, at a waterhole: (1) other herbivores spend more time around the water probably owing to an increased level of vigilance, hence a longer time needed to meet their water requirements, or because the presence of elephants may signal

safety from predators; (2) other herbivores spend shorter time around the water because they are disturbed by elephants' presence and consequently have to leave the waterhole area probably without having met their water requirements (e.g. aggressive interactions leading to a departure), or (3) other herbivores do not change their drinking behaviour.

Hwange National Park (Hwange), Zimbabwe, is a relevant and timely study site to investigate the effects of elephants on other herbivores at waterholes for the following reasons: (1) natural surface-water sources dry up in the dry season when most of the water available to animals is found in few artificially filled waterholes, and surface-water is likely to be a limiting resource; (2) depletion, which occurs at the beginning of the dry season when natural waterholes dry up, can however be neglected at the peak of the dry season when National Park managers pump and maintain a number of waterholes active. Thanks to this quasi-permanent renewal of surface water at the end of the dry season, Hwange is an ideal site to study interference mechanisms; (3) the elephant population has been increasing drastically in Hwange since the mid 1980s reaching an average density of more than two elephants per km^2 over the whole park (Chamaillé-Jammes et al. 2008), and this increase has been correlated to a decrease in some other herbivore populations (Valeix et al. 2007c, 2008). Because elephants gather in high densities near waterholes in the dry season, where they represent 80–90% of the herbivore biomass, and because aggressive interactions between elephants and other herbivores have been documented (Valeix et al. 2007a), an hypothesis of competition for water in this ecosystem has been proposed and insights into the influence of elephants on other herbivores at waterholes is consequently urgently needed.

Materials and Methods

Study area

Hwange covers c. 15,000 km^2 of semi-arid savanna in north-western Zimbabwe (19°00′S, 26°30′E). The vegetation is primarily woodland savanna (64%) and vegetation communities are dominated by *Colophospermum mopane*, *Combretum* spp., *Acacia* spp., *Baikiaea plurijuga* and *Terminalia sericea* (Rogers 1993). Altitude varies from 800 to 1,100 m. The long-term (1928–2005) annual rainfall average is 606 mm but is highly variable (CV ≈ 30%). Most rain fall between October and April. Our study was undertaken at the peak of the dry season (August–October) in 2003, which was a drought with only 474 mm. If elephants have an influence on other herbivores at waterholes, we expected to detect it because of the very dry conditions under which the study was carried out.

Data collection

Our study is based on data collected at nine waterholes located in the northern sector of Hwange. The average diameter of a waterhole is 85 m ± 35 m. In 2003, we regularly monitored (with 12 and 24-h surveys) these waterholes at the peak of the dry season (864 observation hours). We studied the drinking behaviour of nine herbivore species: African buffalo *Syncerus caffer*, giraffe *Giraffa camelopardalis*, impala *Aepyceros melampus*, greater kudu *Tragelaphus strepsiceros*, roan antelope *Hippotragus equinus*, sable antelope *Hippotragus niger*, warthog *Phacochoerus aethiopicus*, blue wildebeest *Connochaetes taurinus*, and plain zebra *Equus quagga*.

For a herd that came to drink, we recorded the time when the first herbivore of the herd started drinking, the time when 50% of the herd started drinking, the time when 50% of the

herd stopped drinking, and the time when the last herbivore of the herd stopped drinking. We then calculated the potential drinking time (PDT), which corresponded to the time a group of animals spent in potential contact with water. For herds up to three herbivores, we calculated the PDT as the difference between the time when the first herbivore of the herd started drinking and the time when the last herbivore of the herd stopped drinking. For herd size above three individuals, we calculated the PDT of the herd as the difference between the time when 50% of the herd started drinking and the time when 50% of the herd stopped drinking. This allowed us to control for herd size. For each herd that came to drink, we recorded the maximum number of elephants that were present at the waterhole while the herd was drinking.

Data analysis

We used a two-step approach to evaluate the influence of elephants on PDT by assessing the influence of (1) the presence/absence of elephants at waterholes, and (2) the abundance of elephants at the waterholes. We first performed Levene's test for equality of variances and then unrelated two-sample *t*-tests on the PDT grouped by the presence/absence of elephants. We then used quantile regressions (Cade et al. 1999; Koenker 2005) to study changes in central tendency while accommodating for variance heteroscedasticity (0.5 quantile regression) and to estimate and test slopes along the "edge" of point clouds (0.9 quantile regression). For each species except wildebeest for which not enough data were available, we performed 0.5 and 0.9 quantile regressions and significant levels were assessed using bootstrapping method (Koenker 2005). These statistical analyses were run with R software using the "quantreg" package (http://www.econ.uiuc.edu/~roger/research/rq/rq.html).

Results

The number of groups that drank at a waterhole during our monitoring effort and information on group sizes are provided in Table 1, as well as the probability of a group attending a waterhole when at least one elephant was present. Detailed information on interactions between elephants and other herbivores at waterholes is provided in Valeix et al. (2007a). More than half the species had a mean PDT significantly longer when there were elephants at the waterhole and the pattern was the same for all species (Fig. 1). When the number of elephants at the waterhole increased, the 0.5 PDT quantile increased significantly for zebra only ($P = 0.020$), and the 0.9 PDT quantile increased significantly for giraffe ($P = 0.044$), kudu ($P = 0.007$) and warthog ($P = 0.023$).

Discussion

The interest of this study was to focus on water in a semi-arid savanna where there are concerns that elephant high densities may have an impact on other species by preventing them from drinking during dry years. If elephant presence, abundance or behaviour would have shortened the time that herbivores can spend at waterholes, we could have considered that herbivores would not have enough time at waterholes to meet their water requirements. However, the results of our study, which was carried out during the second year of a 2-year drought, show that all herbivores spend more time at waterholes when there are elephants.
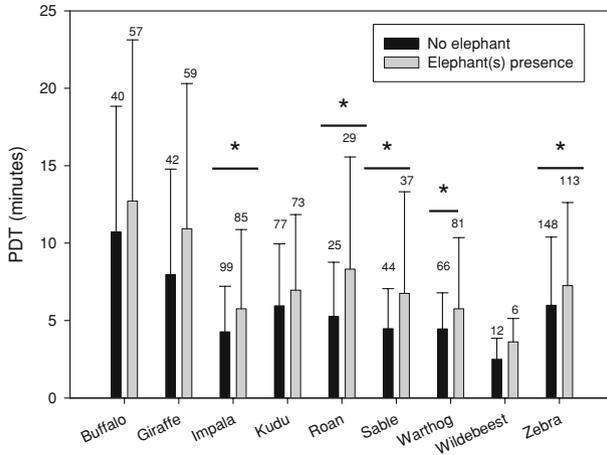
Fig. 1 Potential drinking time (PDT) for all species presented for situations with and without elephants at the peak of the dry season. The number of observations is indicated above the symbols for each species. The level of significance of the two-sample *t*-test is indicated when the test is significant: * $P < 0.05$

Table 1 Number of groups that were monitored while drinking, size of the groups and probability that elephants were present when groups attended a waterhole during the peak of the dry season

Species	Number of groups	Group size mean ± SD (min/max)	Probability of elephant presence (±SD)
Buffalo	97	32 ± 124 (1/1000)	0.57 (±0.04)
Giraffe	101	2 ± 2 (1/11)	0.55 (±0.04)
Impala	184	12 ± 15 (1/71)	0.46 (±0.04)
Kudu	150	5 ± 4 (1/21)	0.49 (±0.04)
Roan	54	2 ± 2 (1/7)	0.54 (±0.06)
Sable	81	4 ± 5 (1/28)	0.40 (±0.04)
Warthog	147	2 ± 1 (1/6)	0.52 (±0.04)
Wildebeest	18	14 ± 15 (1/60)	0.28 (±0.06)
Zebra	261	7 ± 8 (1/61)	0.43 (±0.02)

There is no biological reason why herbivores would drink more when there are elephants and our results therefore suggest that herbivores coming to waterholes when there are elephants either (1) stay longer around waterholes (e.g. wallowing activities) when there are elephants because the presence of elephants probably signals safety from predators or (2) compensate for a reduced intake rate (because of an increased level of vigilance due to the presence of competitors) by staying longer at waterholes probably in order to meet their water requirements. Further research based on direct measure of drinking time from a focal animal sampling approach (Altmann 1974) is needed to disentangle these two scenarios.

Further, the fact that the PDT is not directly and linearly influenced by the abundance of elephants at waterholes for most species could suggest (1) the existence of a threshold in elephant numbers, above which herbivore behaviour changes, or (2) that only elephant presence has an influence (i.e. the behaviour of other herbivores is influenced similarly whether there are 5 or 50 elephants). Examination of the data strongly suggests that (1) few data were obtained at very high elephant abundance (>70 elephants), (2) for the data collected, only elephant presence has an influence. It is possible that the presence of elephants

imports more than their abundance because elephants are very large animals and the presence of only a few elephants may be enough to already strongly influence the behaviour of other herbivores.

The four species (impala, roan, sable and warthog) that showed a significant difference in PDT between elephant absence and presence are species for which there has been evidence that they are more likely to be involved in an interaction with elephants when elephant number at the waterhole is high (Valeix et al. 2007a). This consideration appears to support the scenario whereby other herbivores compensate for a reduced intake rate (because of an increased level of vigilance due to the presence of elephants) by staying longer at waterholes probably in order to meet their water requirements. If this is true, the influence of elephants on PDT demonstrated here is consistent with findings from intra-specific studies. Indeed, at the intra-specific level, where the dominance hierarchy is commonly derived from the number of successful agonistic interactions between individuals (Poisbleau et al. 2006), the intake rate of subordinate individuals decreases as the density of dominant individuals increases and hence the risk of aggression increases (Ens and Goss-Custard 1984; Dolman 1995; Cresswell 1998). At the inter-specific level, many physiological and ecological attributes scale with body size (Peters 1983). Larger species are commonly considered as benefiting from a direct size advantage, having lower costs for interference behaviour, and therefore as being superior to smaller ones in interference competition (Peters 1983; Persson 1985). Because of their very large body size, elephants are thus superior to smaller herbivores in interference competition (Owen-Smith 1988), and consequently it is not surprising that our results suggest increased levels of vigilance for other herbivores when elephants are in the vicinity. Both intra-specific and inter-specific findings strongly suggest a lower intake rate of subordinate individuals/species when dominant individuals/species are in the vicinity. However, our findings differ from those from intra-specific studies in the sense that density of competitors does not appear to play a role in our results (except that few data were obtained at very high elephant abundance suggesting that other herbivores may avoid waterholes when there are too many elephants). By providing insights into the consequences of high levels of aggregation around waterholes on the drinking behaviour of a set of African herbivores, our study constitutes a pioneering approach because it explored at the community level some of the mechanisms that have been demonstrated at the population level (Ens and Goss-Custard 1984; Dolman 1995; Cresswell 1998).

Additionally, it is one of the first studies on interference to focus on drinking behaviour. In the context of interference between individuals during foraging, the forage resource is depleted, whereas in the context of our study, the water in the studied artificially pumped waterholes is not, and competition occurs for access to water (in time and/or space) rather than for water itself. It is also likely that the patch size effect is different. While the whole patch area is available when foraging, only the perimeter of the waterhole is available when drinking. Hence, it is likely that the saturation effect is stronger at waterholes (where the perimeter, and not the surface, determines the access) than at food resource patches. In spite of these differences, the behavioural consequences of animal aggregation around resources appear to be the same.

Under the scenario whereby herbivores compensate for a reduced intake rate by staying longer at waterholes, the potential cost of the presence of elephants at waterholes for other herbivores could be linked to the increased time required for drinking. If herbivores have to spend more time at waterholes, this may have some consequences in terms of (1) higher exposure to higher predation risk as some carnivores preferentially hunt around waterholes (e.g. Schaller 1972), (2) thermoregulation constraints as herbivores tend to avoid spending

long time in open areas in order to avoid elevated heat loads (Demarchi and Bunnell 1993), and (3) time-budget constraints. Indeed, at the end of the dry season, forage resources are not only scarcer but also further from waterhole areas, which are heavily browsed and grazed (Van Rooyen et al. 1994; Parker and Witkowski 1999), forcing herbivores to travel longer distances to find forage (Redfern et al. 2003). In this context, time can become a crucial resource that can be limiting for organisms. However, our results also show that the difference in time spent drinking between situations with no elephant and situations with elephants is not large. Therefore, we suggest that the additional time spent by herbivores when elephants are present is unlikely to affect the population dynamics of these herbivore species, and hence unlikely to be the underlying mechanism to the declines reported for some herbivore populations in Hwange National Park (Valeix et al. 2007c, 2008).

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