
The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores

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Abstract

In African savannas, surface water can become limiting and an understanding of how animals address the trade-offs between different constraints to access this resource is needed. Here, we describe water access by ten African herbivore species in Hwange National Park, Zimbabwe, and we explore four possible determinants of the observed behaviours: water abundance, thermoregulation, perceived predation risk and interference competition. On average, herbivores were observed to drink in 80% of visits to a waterhole. The probability of drinking was higher in 2003 (474 mm) than in 2004 (770 mm), and at the end of the dry season than at its beginning. For larger species, this probability may also be related to risks of interference competition with elephants or other herbivores. For smaller species, this probability may also be related to the perceived risk of predation. We also investigate the time spent accessing water to drink. The influence of herd size and the presence of young on the time spent accessing water for most species suggests that perceived predation risk plays a role. Thermoregulation also affects this time: during the hottest periods, herbivores spend less time in open areas, unless when wind is strong, probably owing to evapotranspired heat loss.

Key words: drinking behaviour, elephants, Hwange National Park, waterholes, Zimbabwe

Résumé

Dans les savanes africaines, l'eau de surface disponible peut devenir un facteur limitant et il est nécessaire de com-

prendre comment les animaux agissent face aux différentes contraintes que pose l'accès à cette ressource. Nous décrivons ici l'accès à l'eau de dix herbivores africains du Parc National de Hwange, au Zimbabwe, et nous explorons quatre facteurs qui sont peut-être déterminants dans les comportements observés: l'abondance de l'eau, la thermorégulation, le risque de prédation ressenti et la compétition/ interférence. En moyenne, on a observé que les herbivores buvaient lors de 80% de leurs visites au point d'eau. La probabilité qu'ils boivent était plus forte en 2003 (474 mm) qu'en 2004 (770 mm), et à la fin de la saison sèche qu'au début. Pour les plus grandes espèces, cette probabilité pourrait aussi être liée aux risques de compétition par interférence avec les éléphants ou d'autres herbivores. Pour les plus petites espèces, cette probabilité pourrait aussi être liée au risque de prédation ressenti. Nous avons aussi étudié le temps passé à se rendre au point d'eau pour y boire. L'influence de la taille du groupe et de la présence de jeunes sur le temps pris par la plupart des espèces pour se rendre au point d'eau laisse penser que la perception du risque de prédation joue un rôle. La thermorégulation affecte aussi cette durée: pendant les périodes les plus chaudes, les herbivores passent moins de temps dans les espaces ouverts, sauf si le vent est fort, probablement à cause de la perte de chaleur par évapotranspiration.

Introduction

Successful management of African savanna ecosystems requires an understanding of the relationship between surface water and herbivore populations (e.g. Owen-Smith, 1996; Redfern *et al.*, 2005; Ryan & Getz, 2005;

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Chamaille-Jammes, Valeix & Fritz, 2007). Previous studies have documented that, in arid and semi-arid savannas, herbivore distribution is influenced by the location of water sources, particularly during the dry season (Western, 1975; Bergstrom & Skarpe, 1999; Redfern *et al.*, 2003). Additionally, as the dry season progresses, these water resources become scarce and patchily distributed, resulting in high levels of animal aggregation near water sources (Thrash, Theron & Bothma, 1995). The consequences of such aggregations on the vegetation surrounding waterholes have been thoroughly studied (e.g. van Rooyen *et al.*, 1994; Parker & Witkowski, 1999), but very few studies have dealt with the behavioural consequences of such aggregations. High mortality occurs in African herbivores during droughts (Dunham, 1994; Dudley *et al.*, 2001), and the creation of waterholes has led to increases in herbivore populations in many protected areas and game ranches (e.g. Davison, 1967). It is therefore conceivable that access to water can potentially limit populations in ecosystems where water is scarce, and knowledge about the possible determinants of this access is of high interest for conservation and management.

In this study, we investigated water access in African herbivores, using surrogate observations to describe: (i) the decision to drink, having arrived in a waterhole area and (ii) for a drinking event, the time spent accessing water. Herbivores may face trade-offs between different constraints when accessing water. Four possible factors are explored here.

Water abundance

During drier periods (dry years or end of the dry season), the probability of drinking when entering a waterhole area should be higher because the probability to find water is lower. Besides, drinking sites as well as foraging patches of acceptable quality are fewer and this situation induces longer travelling distance and longer time spent searching for resources. Consequently, environmental variables influence herbivore time-budgets, which end up more constrained in dry periods. We expect the time spent accessing water to drink to be shorter in drier periods.

Thermoregulation

The study took place in a semi-arid savanna where herbivores face costs linked to high temperatures rather than low (mean temperature: 22.4°C; 25% percentile: 17.6°C;

75% percentile: 28°C), and where waterholes are surrounded by an open area over-utilized and trampled, often referred to as the 'sacrifice area' (Brits, van Rooyen & van Rooyen, 2002). During hot weather, shade from vegetation cover reduces ambient temperature and provides opportunity to avoid elevated heat loads (thermal cover concept; Demarchi & Bunnell, 1993). Consequently, during the hottest periods, the time spent accessing water to drink should be shorter because herbivores should avoid staying in open areas where they are not protected from solar radiation. During windy periods, it is possible that herbivores could afford to stay longer in open waterhole areas as they benefit from evapotranspiration (wind-mediated heat loss). Animal behaviour has major impacts on heat loading, and there is evidence that some herbivores, such as African elephant (*Loxodonta africana*), African buffalo (*Syncerus caffer*) and warthog (*Phacochoerus africanus*) wallow during daytime drinking events to avoid elevated heat loads (Ayeni, 1977).

Perceived predation risk

Perceived predation risk can influence herbivore behaviour and particularly their vigilance behaviour (Hunter & Skinner, 1998). Large herd sizes are considered an advantage for anti predator behaviour because in addition to a risk dilution effect, the probability of an early warning when a predator is in the area is higher (Lima, 1995; Roberts, 1996). It is possible that the same facilitation mechanism occurs at the interspecific level (Morse, 1977; Fitzgibbon, 1990) and that herbivores tend to go to waterholes when other herbivores are already there. The presence of young can also influence the behaviour of a group because young are very vulnerable to predators (Berger, 1991; Burger & Gochfield, 1994). Distance to cover is central in the perception of predation risk by herbivores, and often affects vigilance behaviour (Burger, Safina & Gochfield, 2000). Indeed, vegetation cover can facilitate both concealment and escape from predators (Lima, 1992), but it can also provide camouflage for ambush predators (Hopcraft, Sinclair & Packer, 2005). When perceived predation risk is high, the probability of drinking should be lower, and the time spent accessing water should be longer as more vigilance is expected. Here, we consider that small herd size, small number of elephants and other herbivores around the waterhole, presence of young and close vegetation cover are associated with a high perceived predation risk.

Interference competition

Aggregation of animals induces depletion of resources and may result in interference competition (Wilson & Richards, 2000). Behavioural interactions can be costly either directly, when aggressive interactions are involved, or indirectly, through a reduction in intake rate caused by an increased level of vigilance (Goss-Custard, 1980). Larger species, which have a size advantage in interference behaviours (Peters, 1983), can be considered as keystone-competitors (*sensu* Bond, 1993). This may be the case for elephants, the largest terrestrial mammals, which may represent a major source of aggressive interactions (Berger & Cunningham, 1998; Valeix, Chamaille-Jammes & Fritz, 2007a). Therefore, under an interference competition scenario, the probability of drinking should decrease and the time spent accessing water should increase, when the number of elephants and other herbivores at the waterhole increases.

Methods

The study took place in Hwange National Park (HNP hereafter), which covers *c.* 15,000 km² of semi-arid savanna in the northwestern Zimbabwe (19°00'S, 26°30'E; Fig. 1). The long-term (1928–2005) annual rainfall average is 606 mm with most rain falling between October and April, but annual rainfall is highly variable (CV \approx 30%). The year is divided into a wet and a dry season (respectively November–April and May–October). Naturally, there is no permanent surface water in HNP: three ephemeral rivers and waterholes hold rainwater in

the rainy season and at the beginning of the dry season (Fig. 1). When HNP was created, no water was available at the peak of the dry season in dry years (Davison, 1967). National Parks opted for water management in the dry season by pumping underground water. Most of the water available to animals in the dry season is found in these artificially filled waterholes (Fig. 1). Under average climatic conditions (annual rainfall of 606 mm), 7.6% of the park occur within 2 km of a water source, 26.9% between 2 and 5 km, 34.4% between 5 and 10 km, 24.4% between 10 and 20 km and 6.7% over 20 km (Chamaille-Jammes, Fritz & Murindagomo, 2007).

We regularly monitored twelve waterholes in 2003 (19.44 hours of observation) and nine waterholes in 2004 (18.48 hours of observation). Information about the vegetation surrounding each monitored waterhole is provided in Table 1. The monitoring lasted throughout the dry season, which can be divided between the beginning of the dry season from May to July, and the end of the dry season from August to October. The two study years differed in terms of rainfall (474 mm in 2003 and 770 mm in 2004). We monitored each waterhole twice a month, with a 24-h monitoring effort coinciding with the full moon and a 12-h monitoring effort when no moon was present. We previously showed that for all herbivores, except elephants, majority of the individuals come during the daytime period (Valeix *et al.*, 2007a); hence, we did not correct for the potential influence of moonlight on predator visibility or on the nocturnal activity for certain species (e.g. Ryan & Jordaan, 2005). Each 24-h survey was run from noon of one day to noon of the following day and each 12-h survey from 06.00 to 18.00 hours of the same day. The monitoring was

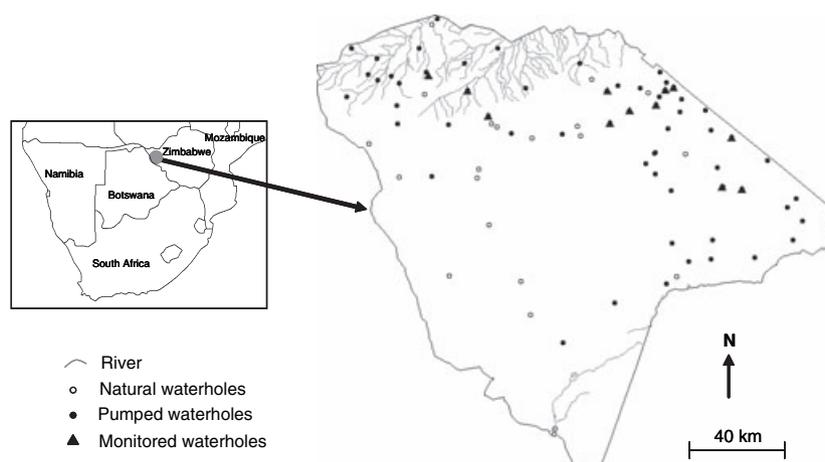


Fig 1 Map of Hwange National Park showing surface water sources. The river network and most of the natural waterholes dry up during the dry season

Table 1 Description of the vegetation surrounding monitored waterholes

Waterhole	Vegetation structure	Dominant tree/bush species
Deteema	Woodland/thicket	Mixed
Masuma	Woodland/thicket	<i>Colophospermum mopane</i> (J. Kirk ex Benth.) J. Léonard
Shumba	Woodland bushland mosaic	<i>Colophospermum mopane</i>
Guvalala	Bushland	<i>Acacia</i> spp./ <i>Baikiaea plurijuga</i> Harms
Nyamandhlovu	Bushed grassland	<i>Acacia</i> spp./ <i>Combretum</i> spp.
Sedina	Bushed grassland/wooded bushland	<i>Burkea africana</i> Hook./ <i>Combretum</i> spp.
Kaoshe	Wooded bushland/thicket	<i>Colophospermum mopane</i> / <i>Combretum</i> spp.
Boss Long One	Bushland/woodland	<i>Terminalia sericea</i> Burch. ex DC./ <i>Baikiaea plurijuga</i>
Balla Balla	Woodland	<i>Baikiaea plurijuga</i>
Kennedy 1	Bushed grassland/wooded bushland	<i>Combretum</i> spp./ <i>Terminalia sericea</i>
Ngweshla	Bushed grassland/bushland	<i>Combretum</i> spp./ <i>Guibourtia coleosperma</i> (Benth.) J. Léonard
Samavundhla	Bushed grassland/bushland	<i>Combretum</i> spp./ <i>Guibourtia coleosperma</i>

done from a tourism platform, from a hide in a tree, or from a car parked at a distance from the waterhole so as not to disturb the animals. We studied ten herbivore species: three browsers or mixed-feeders (giraffe *Giraffa camelopardalis*, impala *Aepyceros melampus* and greater kudu *Tragelaphus strepsiceros*), three grassland grazers (waterbuck *Kobus ellipsiprymnus*, blue wildebeest *Connochaetes taurinus* and Burchell's zebra *Equus burchelli*) whose habitats are often associated with waterholes, and four grazers whose habitats are less associated with waterholes (buffalo, warthog and two open woodland grazers: roan antelope *Hippotragus equinus* and sable antelope *Hippotragus niger*).

For all herbivores entering a waterhole area, which was defined as a circle of 100-m radius, we recorded whether the herbivores drank or not. If they drank, we measured the time spent accessing water as the difference between the time when the herd entered the waterhole area and the time when the first herbivore of the herd drank. We recorded data relevant to test thermoregulation hypotheses. Every 6 h, we recorded the temperature and we coded wind intensity as an integer between zero (no wind) and three (strong wind). This allowed allocating to each observation the closest temperature record and calculating for each monitoring session the mean wind intensity. Because HNP has populations of large carnivores, we also recorded data relevant to test perceived predation risk hypotheses: herd size, presence of young, distance to cover for the four cardinal and four ordinal directions. We finally recorded data relevant to interspecific anti-predation facilitation hypotheses and interspecific interference competition hypotheses: number of elephants and other herbivores at the waterhole when the focal herd arrived.

For each species, we calculated the probability of drinking once in the waterhole area by using a logistic regression model. For herds that drank, we also calculated the mean time spent accessing water. To identify the factors influencing the decision to drink and the time spent accessing water, we then performed a backward step-wise selection procedure with successive removals of variables for which $P > 0.05$. The variables were the year (2003 or 2004), the season (beginning of the dry season or end of the dry season), the temperature, the mean wind intensity, the herd size, the presence of young, the minimum distance to vegetation cover, the number of elephants at the waterhole, and the number of other herbivores (except elephants) at the waterhole. We analysed the interactions of the variables with year and with season but none was significant. All statistical analyses were generalized linear model performed with SAS software (version 8.2, SAS Institute Inc., Cary, NC, USA), using 'GENMOD' procedure for binomial distributed data (decision to drink) or for Poisson distributed data (time spent accessing water to drink), then correcting the models for over-dispersion by a scaling function: deviance⁻¹ (Cox & Snell, 1989; Firth, 1991).

Results

Probabilities of drinking once in a waterhole area differed between species, and ranged from 0.61 for giraffe and wildebeest to 0.91 for buffalo (Fig. 2). For most species, herds drank in <80% of the visits to waterholes (Fig. 2). These first results highlighted the need to understand the mechanisms that drive the decision to drink or not at a

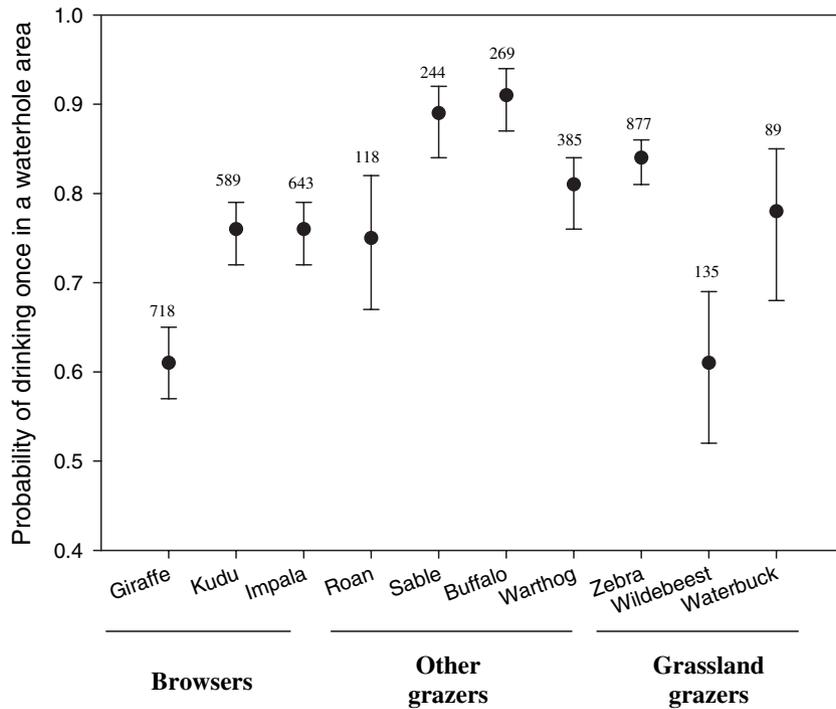


Fig 2 Probability of drinking once in a waterhole area for all studied herbivore species. The results are the estimates from logistic regression models [\pm Wald 95% confidence interval (Cox & Snell, 1989)]. The number of observations is indicated above the symbols for each species. Note that, on average, herbivores were observed to drink in *c.* 80% of the visits to waterholes, suggesting that on some occasions some herds might have been discouraged from drinking

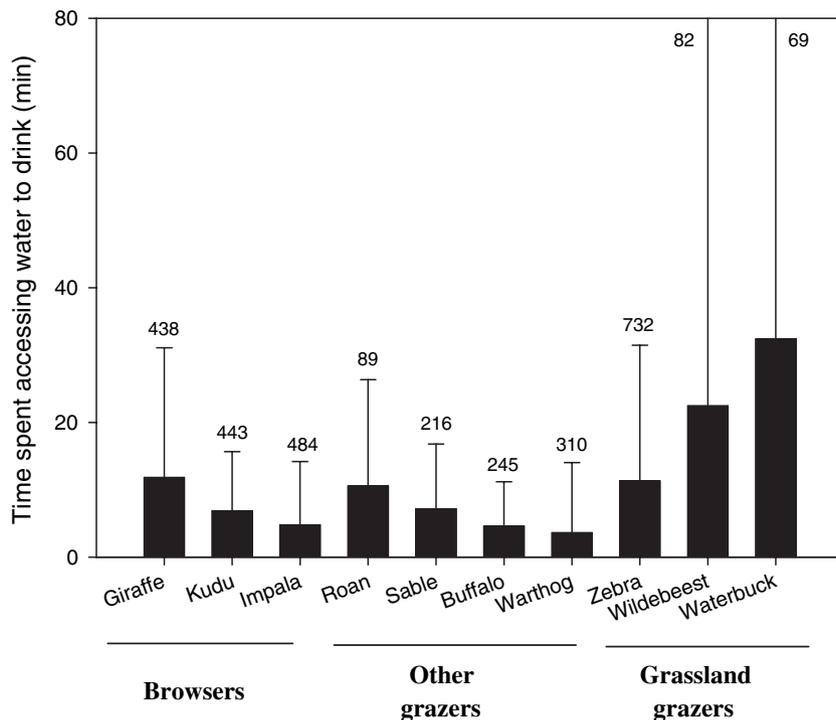


Fig 3 Mean time spent accessing water to drink (with SD) for all studied herbivore species. The number of observations is indicated above the symbols for each species. Note that the variability in the time spent accessing water to drink was rather high, and that this time was rather short for species other than grassland grazers (range: 3–12 min)

given waterhole. For species other than grassland grazers, the mean time spent accessing water ranged from 3 min for the warthog to 12 min for the giraffe (Fig. 3). Because

the variability in the time spent accessing water to drink was quite high, there was a need to investigate what influenced it.

Probabilities of drinking were higher in 2003 than in 2004 (impala, warthog, wildebeest and zebra), and they were higher at the end of the dry season than at the beginning of the dry season (impala, kudu, roan, warthog and zebra) (Table 2). This was expected, as 2003 was drier than 2004, and as the end of the dry season is drier than the beginning. As expected also, the time spent accessing water to drink was usually shorter in 2003 than in 2004 (warthog and zebra), and was usually shorter at the end of the dry season than at the beginning (warthog and wildebeest) (Table 3).

The major role of thermoregulation seemed to be for the time spent accessing water to drink. As expected, for most species, this time decreased as temperature increased, and it increased as wind intensity increased (Table 3).

Perceived predation risk seemed to play a role in the probability of drinking for all species except buffalo, roan and zebra (Table 2), as well as in the time spent accessing water to drink for all species except kudu and wildebeest (Table 3). As expected, when the herd size increased, the probability of drinking increased (giraffe,

Table 2 Results of the logistic regressions modelling the probability of drinking once in a waterhole area for all the studied herbivore species

(n)	Year ^a	Season ^a	Temperature ^b	Wind ^b	Herd size ^b	Juvenile ^a	Distance cover ^b	Nb herbivores ^b	Nb elephants ^b
Giraffe (718)					+		-		-
Kudu (589)		End**			+		-		
Impala (643)	2003*	End***		-			-		
Roan (118)		End*							-
Sable (244)					+			-	
Buffalo (269)			-						
Warthog (385)	2003***	End***	+			No juv*			
Zebra (877)	2003**	End*		-					
Wildebeest (135)	2003*				+		-		
Waterbuck (89)							-		

Results are issued from chi-squared tests. Only significant variables are shown.

* $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$.

^aFor categorical variables, the class with higher estimate is indicated (ex: 'end' indicates that the probability of drinking is higher at the end of the dry season than at the beginning of the dry season).

^bFor continuous variables, +/- indicates the sign of the estimate.

Table 3 Results of the regressions modelling the time spent accessing water to drink for all the studied herbivore species

(n)	Year ^a	Season ^a	Temperature ^b	Wind ^b	Herd size ^b	Juvenile ^a	Distance cover ^b	Nb herbivores ^b	Nb elephants ^b
Giraffe (438)		End***	-	+	-		+		+
Kudu (443)							+		
Impala (484)	2003**			+			+		
Roan (89)				-				+	
Sable (216)				-			+		
Buffalo (245)			-			Juv**	+		
Warthog (310)	2004***	Begin*	-	+		Juv***	+		+
Zebra (732)	2004***		-	+		Juv*	+		+
Wildebeest (82)		Begin***		+					
Waterbuck (69)			-		-	Juv**			

Results are issued from chi-squared tests. Only significant variables are shown.

* $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$.

^aFor categorical variables, the class with higher estimate is indicated (ex: 'end' indicates that the time spent accessing water is longer at the end of the dry season than at the beginning of the dry season).

^bFor continuous variables, +/- indicates the sign of the estimate.

kudu, sable and wildebeest) (Table 2), and the time spent accessing water to drink decreased (giraffe, roan, sable and waterbuck) (Table 3). When there were young in a herd, the time spent accessing water to drink was longer (buffalo, warthog, waterbuck and zebra) (Table 3). None of the statistical relationships suggested an interspecific benefit in terms of reduced perceived predation risk. However, when the minimum distance to vegetation cover increased, the probability of drinking decreased (giraffe, impala, kudu, waterbuck and wildebeest) (Table 2), and the time spent accessing water to drink increased (buffalo, giraffe, impala, sable, warthog and zebra) (Table 3).

The risk of interference competition influenced the decision to drink for only three species (Table 2). Giraffe and roan reacted negatively to the abundance of elephants, and sable reacted negatively to the abundance of other herbivores, excluding elephants (Table 2). As the number of elephants increased, giraffe, warthog and zebra spent more time accessing water (Table 3). As the number of other herbivores increased, only roan spent more time accessing water (Table 3).

Discussion

This work is one of the first thorough studies of water access in wild herbivores at the community level. We showed that herbivores do not always drink when they come to a waterhole area. This result, which might not be surprising for grassland grazers that often come to waterholes areas to graze and not to drink, becomes more complex to understand for browsers and for open woodland grazers, if we consider that they come to waterhole areas mainly to drink. This could indicate that some herds were discouraged from drinking by some factors. We also showed that when one factor was playing a significant role for some species, the patterns were consistent for all species, which gave insights into the collective behaviour of herbivores at waterholes.

Water abundance

Our results confirmed that when water abundance decreases, the need to drink becomes more crucial. This was particularly the case for grazers (roan, warthog, wildebeest and zebra), which is consistent with the fact that grazers are highly water dependent species (Western, 1975).

Thermoregulation

Thermoregulation did not influence the decision to drink once in a waterhole area. However, thermoregulation seemed to play an important role in the time spent accessing water. Consistently with the thermal cover concept (Demarchi & Bunnell, 1993), during hotter periods, herbivores avoided staying in open areas where solar radiations were at a maximum. Interestingly, this was particularly the case for the largest herbivores (giraffe, buffalo and zebra). This is consistent with the fact that body size has a major effect on heat balance with large animals heating and cooling less rapidly than small ones (Peters, 1983). Buffalo is a species also known for wallowing during daytime drinking events (Ayeni, 1977). Regarding wind intensity, the patterns observed suggested that herbivores stayed more in open areas when wind was strong to facilitate evapotranspired heat loss.

Perceived predation risk

Recent works have suggested that larger species are less prone to predation than smaller species (Sinclair, Mduma & Brashares, 2003; Radloff & du Toit, 2004). If we exclude giraffe, which could be considered as an exception (drinking is the only activity when it is vulnerable to predators because of its posture when drinking), this could be the reason why the largest species (buffalo, roan and zebra) were the species that did not show any perceived predation risk specific influence on their decision to drink. The 'group size effect' seemed to operate at the intraspecific level (Lima, 1995; Roberts, 1996). The presence of young influenced the time spent accessing water, suggesting an increased vigilance level. This corroborates that females with juveniles are generally more alert than females without young (Burger & Gochfield, 1994). Results were contrary to our predictions regarding the distance to cover probably because further the vegetation cover, lower the perceived predation risk is, and more the time herbivores spend in the area, taking the opportunity for other activities (e.g. social display is more efficient in open areas). Interestingly, the species sensitive to the distance to cover for their decision to drink were some of the smallest ones (plus the giraffe), which was consistent with their higher vulnerability to predation (Sinclair *et al.*, 2003). The existence of a group size effect and the suggested change in behaviour when there were

young indicated that perceived predation risk acted as a regulator of behaviour at waterholes. No anti-predation facilitation at the interspecific level was suggested by our results.

Interference competition

The trends observed in this study suggested behavioural adjustments to minimize interspecific interference competition for only a few species. It is interesting to note that the three species that made the decision not to come to waterholes when these were occupied by many elephants or other herbivores were among the largest species of the herbivore community studied. In addition, giraffe and roan are known to be less water dependent than other species (Western, 1975). For the time spent accessing water to drink, it generally increased with the number of other herbivores, which suggested that either a lot of time was devoted to vigilance activities and to potential interactions, or that herbivores engaged in other activities while waiting to access the water. In HNP, most herbivore species have declined over the past 20 years parallel to the increase in the elephant population, and questions about the potential competition for water between elephants and other species have arisen (Valeix *et al.*, 2007b). This study suggests that elephant abundance at waterholes does not prevent other herbivores from accessing water.

Although all our findings seem consistent across species, the conclusions as to which constraints prevail are not straightforward. However, we can try to derive some general rules and mechanisms to describe these behaviours: (i) for most species, the decision to drink depends largely on water abundance; (ii) for larger species, this decision may be modulated by potential interference competition with elephants and other herbivores; (iii) for smaller species, this decision may be modulated by perceived predation risk; and (iv) these factors still hold when considering the time spent accessing water for herds that come and drink, but thermoregulation may then play an important role, as herbivores need to avoid heavy heat loads. This study calls for similar approaches in sites with different sets of constraints (e.g. high level of predation versus no predation, natural systems versus systems with artificial water supply). This would provide essential information for management, particularly in water supplemented ecosystems.

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