BEHAVIORAL ECOLOGY

Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes

Marion Valeix · Simon Chamaillé-Jammes · Hervé Fritz

Abstract Scarcity of resources may result in high levels of animal aggregation; interference competition can occur in such a scenario and play a role in resource acquisition. Here, we test the hypothesis that animals could minimize interference competition by shifting their temporal niches in relation to competitors. In Hwange National Park, Zimbabwe, we monitored waterholes in order to study agonistic interactions between elephants and other herbivore species. We also used a long-term data set from a yearly survey of waterhole attendance by herbivores to evaluate the influence of the presence of elephants on the use of waterholes by other herbivore species. Our results show that in drier years, waterholes are crowded with elephants early in the afternoon. In general, the species most affected by interference competition with elephants shift their temporal niches at the waterholes, thus maintaining a constant temporal overlap with elephants. The species less affected by interference competition with elephants show no temporal niche shifts and increase their temporal overlaps with elephants at waterholes, as predicted from a noncompetition hypothesis. This study provides evidence that interference competition with a behaviorally dominant large species influences the temporal niches of smaller species, and suggests that the potential costs associated with interference between elephants and other herbivores at waterholes are linked to shifts in diurnal activities rather than interactions and water acquisition itself.

Keywords Behavioural adjustments · Hwange National Park · Keystone competitor · Niche overlap · Zimbabwe

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Introduction

Interspecific competition is a central mechanism that governs community structure (Schoener 1983; Chase et al. 2002). The competitive exclusion principle (Hardin 1960) traditionally states that two species that compete for the same resources cannot stably coexist because one of the two competitors will always have an advantage over the other that leads to extinction of the second competitor in the long run. However, in the real world, where evolution comes into play and where there is spatial heterogeneity, multiple resource competition and possibility of emigration, this will lead to an evolutionary shift of the inferior competitor towards a different ecological niche. As a consequence, interspecific competition is considered to be a major selective force that explains niche partitioning (e.g., Tokeshi 1999) as well as character displacements and behavioral differences between species (Abrams 1986; Abrams and Chen 2002).

Animals can compete either by reducing the availability of a shared resource to other animals (exploitation com-

petition) or by reducing the ability of other animals to make use of a shared resource through behavioral interactions (interference competition) (e.g., Tokeshi 1999). Interference competition has been understudied compared to exploitation competition, even though it may be just as important (Adler and Mosquera 2000; Amarasekare 2002). Interference competition has usually been studied at the population level, exploring the role of intraspecific interference (Ens and Goss-Custard 1984; Dolman 1995; Cresswell 1998). However, interference competition between species also has the potential to structure communities (Case and Gilpin 1974; Palomares and Caro 1999; Caro and Stoner 2003). Larger species may benefit from a direct size effect, receive lower costs from interference behavior, and may therefore be superior to smaller ones in interference competition, thus illustrating a case of asymmetrical competition (Peters 1983; Persson 1985). It is therefore possible that larger species play more important roles than smaller species in structuring communities via interference competition for resources, and they can be considered to be keystone competitors (sensu Bond 1993).

When resources become scarce, animals are forced to aggregate near them, and it is likely that high levels of aggregation lead to interference behavior, in addition to an increase in exploitation competition (Vahl et al. 2005). It is of interest to understand the response and the behavioral adaptation of animals to this phenomenon. Apart from the extreme case of interspecific killing (Palomares and Caro 1999), interference competition may result in either a reduced intake rate or in a change in ecological niche by the impacted animals (Goss-Custard 1980). Indeed, animals may choose to exploit poorer quality habitats or suboptimal activity periods because limitation of spatial or temporal overlap reduces the effects of interference competition. In this study, we focus on time as a real niche dimension over which animals can minimize interference competition (Carothers and Jaksic 1984; Loreau 1989; Kotler et al. 1993; Ziv et al. 1993; Albrecht and Gotelli 2001). We test the hypothesis that species affected by interference competition adjust their behavior and shift their temporal niches in order to avoid increasing their temporal overlaps with the competing species.

In African arid and semiarid savannas, as the dry season progresses, surface water resources dry up or become depleted, resulting in scarcity and consequently in high levels of animal aggregation (Trash et al. 1995). African savannas and their associated herbivore communities provide the opportunity to study interference competition for water and its impact on temporal niches at waterholes. African herbivore communities are extremely diverse, which facilitates comparison of species in terms of different costs associated with interference competition for water due to different water requirements and uses (Bothma 1989), as well as differences in distances traveled between water and food resources (Redfern et al. 2003). African herbivore communities also allow the role of a potential keystone competitor, the African Elephant *Loxodonta africana*, to be studied (Weir and Davison 1965; Berger and Cunningham 1998).

In this study, we analyze the influence of elephant presence on the attendance of other herbivore species at waterholes in Hwange National Park, Zimbabwe. We expect a temporal niche shift in the herbivore species most likely to be affected by interference competition with elephants. Thus we expect that species will reduce temporal overlaps with elephants at waterholes by arriving earlier or later than elephants. We first document the agonistic interactions between elephants and other herbivore species at waterholes. We then assess the temporal niche patterns of herbivore species at waterholes and their temporal overlap with elephants to investigate the occurrence of behavioral adjustments in response to interference competition.

Methods

Study site

The study site is Hwange National Park, which covers ~15,000 km^2 of semiarid savanna in northwestern Zimbabwe (19°00′ S, 26°30′ E). The long-term mean annual rainfall is 606 mm, which falls primarily between October and April. The surface water available to animals is found in natural as well as artificially filled waterholes. The amount of rainfall determines the number of natural waterholes with water. Natural waterholes dry up in the dry season when most of the water available to animals is found in few artificially filled waterholes. Animals gather at high densities near waterholes in the dry season, and elephants represent 80–90% of the herbivore biomass at waterholes. There is no waterhole without elephants in Hwange National Park, which prevented us from using real control waterholes. Depletion, which occurs at the beginning of the dry season when some natural waterholes dry up, is greatly reduced at the peak of the dry season when the Zimbabwe Parks and Wildlife Management Authority pumps a number of waterholes and keeps them active. Thanks to this quasi-permanent renewal of surface water at the end of the dry season, which is the critical period of the year for herbivores in terms of water acquisition, exploitation competition can be neglected and Hwange National Park is an ideal site to study interference mechanisms. We studied the potential influence of elephants on ten other herbivore species: three browsers (giraffe *Giraffa camelopardalis*, impala *Aepyceros melampus*, and greater kudu

Tragelaphus strepsiceros), two woodland grazers (roan antelope *Hippotragus equinus*, and sable antelope *Hippotragus niger*) and five grassland grazers (African buffalo *Syncerus caffer*, warthog *Phacochoerus africanus*, waterbuck *Kobus ellipsiprymnus*, blue wildebeest *Connochaetes taurinus*, and Burchell's zebra *Equus burchelli*).

Interference

We regularly monitored (with 12 h and 24 h surveys) 12 waterholes in 2003 (1,944 observation hours) and nine waterholes in 2004 (1,848 observation hours) to document interference competition at waterholes. Waterholes were monitored throughout the dry season, from early May to late October, when the first significant rains fell. We recorded all interactions between elephants and other herbivore species that occurred in a perimeter of 100 m from the waterholes. Interspecific interactions other than with elephants were negligible. Interactions included active interference involving agonistic interactions ranging from intimidation to an aggressive chase, as well as passive interference (Table 1). We defined an interaction as being either noncostly or costly (Table 1). Hereafter, the use of the term ''interaction'' will refer to any interaction between elephants and other herbivores in a waterhole area.

The individuals in a group did not behave independently: when a group was involved in an interaction, the majority of the individuals were actually involved (Table 2), and the individuals involved always behaved similarly. For all species except zebra, the probability of being involved in an interaction with an elephant was independent of group size ($P > 0.05$). In the analyses, we therefore considered the group to be the statistical unit, and the response of the majority of individuals in a group determined the response for the whole group.

Three binomial variables have been used to reflect herbivore behavior probabilities when elephants are at

Table 2 Information on the sizes of the groups involved in interactions with elephants, and on the proportions of individuals actually involved

Species	Number of interactions	Group size, mean ± SD (min/max)	Individuals involved (%), mean ± SD
Buffalo	29	37.6 ± 103.9 (1/480)	75 ± 39
Giraffe	37	3.0 ± 3.1 (1/11)	88 ± 22
Impala	41	9.0 ± 8.4 (1/31)	86 ± 27
Kudu	52	4.6 ± 2.7 (1/13)	87 ± 27
Roan	12	3.2 ± 2.5 (1/8)	83 ± 31
Sable	15	4.1 ± 4.8 (1/14)	94 ± 19
Warthog	25	3.3 ± 1.9 (1/9)	87 ± 24
Waterbuck	4	3.3 ± 1.0 (1/4)	88 ± 25
Wildebeest	5	21.6 ± 19.4 (1/42)	85 ± 34
Zebra	92	10.1 ± 10.7 (1/54)	83 ± 29

waterholes: group coming to a waterhole, group involved in an interaction, and group involved in a costly interaction. The coding used was as follows:

1. Group coming to a waterhole = 1 if the group arrived at a waterhole when there were elephants (at least one), and = 0 if the group arrived at a waterhole when there was no elephant.
2. Group involved in an interaction = 1 if the group arrived at a waterhole when at least one elephant was present and was involved in any interaction (passive or active, costly or not), and = 0 if the group arrived at a waterhole when at least one elephant was present and no interaction occurred.
3. Group involved in a costly interaction = 1 if the group arrived at a waterhole when at least one elephant was present and was involved in a costly interaction, and = 0 if the group arrived at a waterhole when at least one elephant was present and either was not involved

Table 1 Description of the behaviors used to categorize interactions

	Corresponding behaviors
Nature of the interaction	
No interaction recorded	No specific action by the elephant and no specific reaction from the other herbivore. This was also the case when the herbivore only lifted its head with the arrival of an elephant
Passive	No specific action by the elephant, but the behavior of the herbivore changed drastically. In most cases, the herbivore quickly left the waterhole with the arrival of an elephant
Active	Either the elephant intimidated the other herbivore (threatened it with trumpeting and flapping ears), or it aggressively chased it
Consequence of the interaction	
Noncostly	The herbivore either did not change its behavior in response to intimidation or chasing by the elephant, or it moved several meters away and then continued its initial activity
Costly	The herbivore was prevented from drinking by the elephant for a long time (>15 min), or the interaction resulted in the departure of the herbivore from the waterhole area

in an interaction or was involved in a noncostly interaction.

These were the variables used in further analysis. To test whether a behavior probability depended on elephant abundance, we calculated the probability of a group being involved in an interaction or in a costly interaction as a function of the number of elephants at the waterhole when the interaction occurred.

We performed logistic regressions (Cox and Snell 1989) to calculate these different probabilities as well as their Wald's confidence interval, which represent risks of interaction. Statistical analyses were performed using a generalized linear model generated with SAS software (version 8.2) (SAS Institute Inc. 1999), using the ''GEN-MOD'' procedure for binomial distributed data.

Temporal niche

We used a long-term data set resulting from the regular monitoring of waterholes to document temporal niches at waterholes. This regular monitoring consisted of annual 24-h counts during the full moon occurring at the peak of the dry season (end of September to beginning of October). At this time of the year daylight lasts ~12 h 10 min (annual range: 10 h 50 min to 13 h 10 min). Data on arrival times was available for 1967, 1973, 1975, 1976, and from 1994 to 2005 (1997 data was not included in the analyses because exceptional rain occurred during the count, which provided an abnormal situation where only a few animals came to drink). As only information on group arrival time was available, the temporal niche at waterholes was approximated by the arrival time at waterholes. Each year, 57 (± 23 SD) waterholes were monitored. The average temporal distribution of individuals attending waterholes over a 24-h period calculated across all years for all individuals showed that, for all species except elephants, most of the individuals come during the daytime period, i.e. between 6 h and 19 h (Fig. 1).

Because on average 91.7% (range: 81.7% for the buffalo, 99.6% for the warthog) of the individuals of the studied herbivore species (other than elephants) arrived at waterholes during the daytime period (Fig. 1), we used only the daytime period in the following analyses. As the individuals in a group do not behave independently, we used the group and not the individual as the statistical unit in subsequent analyses.

We calculated the mean number of elephants per waterhole per day for each year. For each species, we calculated the mean arrival time at waterholes by year to assess whether herbivore species shifted their temporal niches in response to elephants. We studied time using

linear statistical methods rather than circular statistical methods (Fisher 1993) because we considered the daytime period only. We also calculated the species niche breadth for each year using the Shannon–Wiener index ($-\Sigma_i \, p_i \cdot$ log p_i, where p_i is the proportion of all individuals that attended the waterholes each hour i) (Hanski 1978). The larger the index, the broader the niche. In our context, the niche breadth is a measure of synchrony in the behavior of groups. Finally, for each herbivore species, we estimated the temporal overlap with elephants by calculating the Schoener indices of niche overlap ($O_{12} = \Sigma_i$ min (p_{1i}, p_{2i}), where p_{1i} is the proportion of all individuals of species 1 that attended the waterholes during each hour i) (Schoener 1968; Hanski 1978). Temporal overlap between species 1 and 2 is complete when $O_{12} = 1$, and it is null when $O_{12} = 0$.

We first analyzed the influence of the annual rainfall—calculated as the rainfall that fell from October the previous year through September that year (averaged across three climatic stations in the northern part of the park) and used as a proxy for surface water availability—on elephant attendance at waterholes, by performing a set of linear regressions (Zar 1984): the mean number of elephants per waterhole per day, the mean arrival time of elephants at waterholes, and the niche breadth of elephants at waterholes were regressed on the annual rainfall. We then analyzed the influence of elephant presence on the attendances of other herbivore species at waterholes. To test whether a species would shift its temporal niche in response to changes in elephant attendance at waterholes, we regressed the mean arrival time of each herbivore species against the mean arrival time of elephants, and we regressed the niche breadth of each herbivore species against the mean arrival time of elephants at waterholes. Finally, we analyzed temporal overlaps between elephants and other herbivore species by performing a regression of the temporal overlaps against the mean number of elephants per waterhole per day. Statistical analyses were linear regressions performed with SAS software (version 8.2) (SAS Institute Inc. 1999), using the ''REG'' procedure.

Results

Elephant attendance at waterholes

Elephant numbers at waterholes were higher during drier years (Fig. 2a; mean number of elephants = 367.29 – 0.36 × annual rainfall; $F_{(1,13)} = 7.7$; $P = 0.016$; $r^2 = 0.37$). Moreover, mean arrival time shifted towards earlier times of the day with decreasing rainfall (Fig. 2b; mean arrival

Fig. 1 Average temporal
distribution of individuals
attending waterholes over a
24-h period calculated across all
years for all individuals. Left of
the *dotted line* is the daytime
period (between 6 h and 19 h).
Apart from elephants,
herbivores use waterholes
almost exclusively during the
daytime period. Further
analyses thus consider the
daytime period only
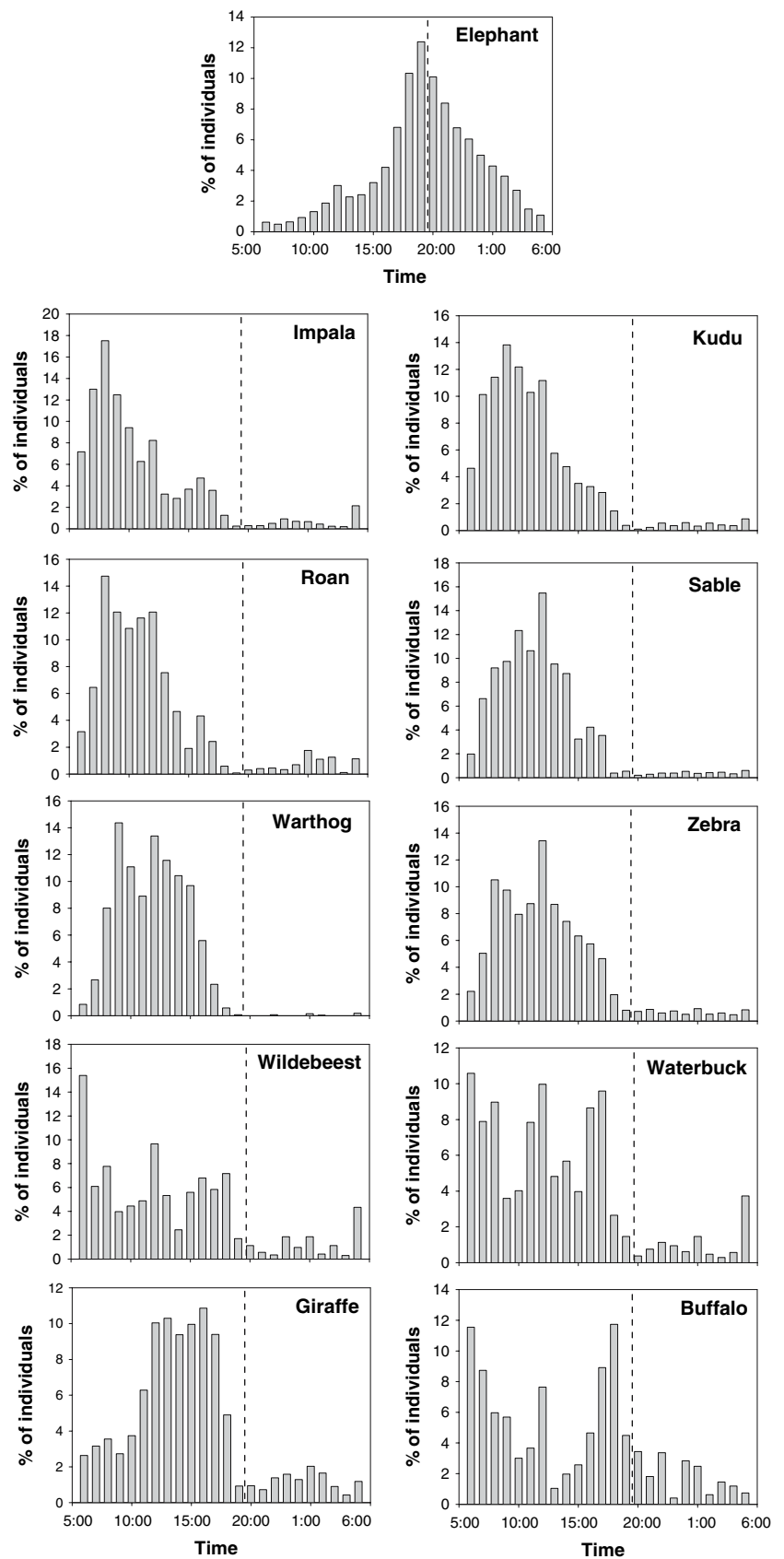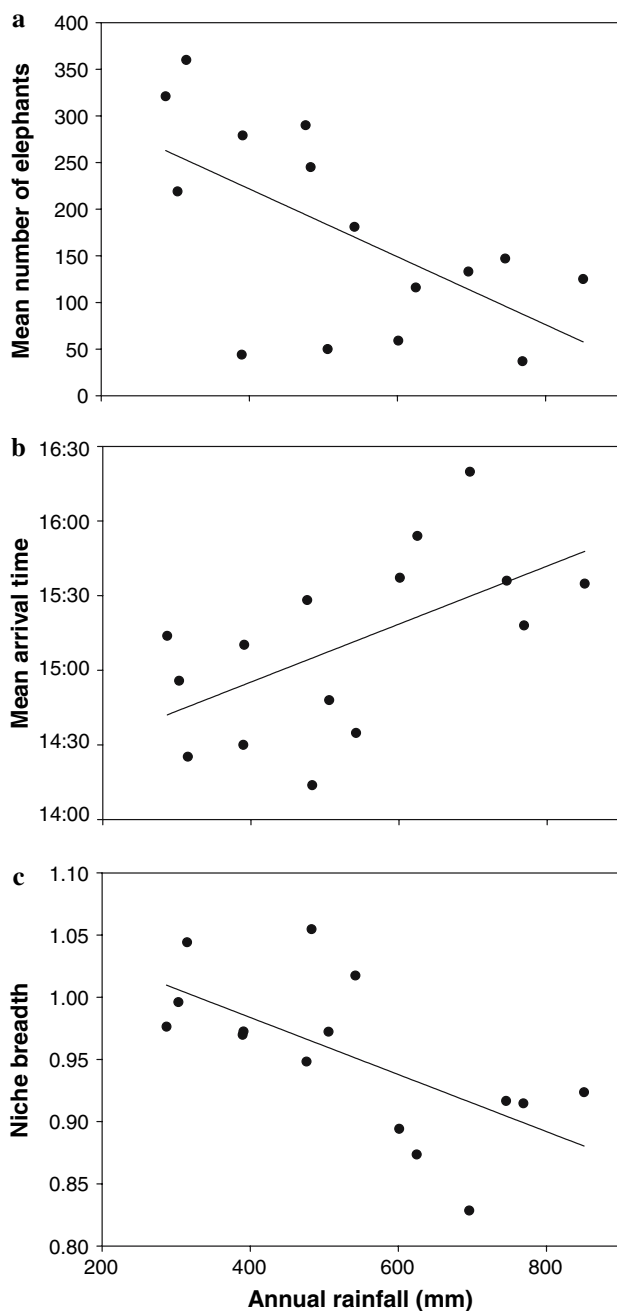
Fig. 2a–c Relationship between annual rainfall and **a** the mean number of elephants per waterhole per day; **b** the mean arrival time of elephants at waterholes; **c** the niche breadth of elephants at waterholes. Figure refers to daytime data only

time = $14.14 + 0.002 \times$ annual rainfall; $F_{(1,13)} = 6.7$; $P = 0.022$; $r^2 = 0.34$). Mean arrival time ranged from 14:14 (SD = 3:24) to 16:20 (SD = 2:18) (Fig. 2b). Finally, elephants had a broader temporal niche in drier years (Fig. 2c; niche breadth = $1.077 - 0.0002 \times$ annual rainfall; $F_{(1,13)} = 10.5$; $P = 0.006$; $r^2 = 0.45$). Thus, the drier the year, the more waterholes are crowded with elephants earlier in the afternoon.

Interference

During the study period (2003–2004), we recorded a total of 312 interactions. More interactions were recorded in 2003 than 2004 (261 and 51 interactions respectively), which was consistent with increased elephant attendance at waterholes in 2003, the drier year (2003 received only 474 mm whereas 2004 received 770 mm). The 312 interactions involved 268 groups, as some groups got involved in several interactions. For all species, the probability of a group attending a waterhole when at least one elephant was present was much higher in 2003 than in 2004 (Table 3). Because the probabilities of being at waterholes with elephants were extremely low in 2004, we analyzed the interference phenomenon based on 2003 data only. Hereafter, we only considered situations where groups arrived

Table 3 Probabilities that elephants were present when various groups attended a waterhole

| Species	2003	2004
Impala	0.41 (0.36–0.46)	0.02 (0.01–0.04)
Kudu	0.43 (0.38–0.48)	0.04 (0.02–0.07)
Roan	0.59 (0.50–0.68)	0
Sable	0.43 (0.36–0.51)	0.01 (0–0.09)
Warthog	0.51 (0.46–0.57)	0.02 (0.01–0.05)
Zebra	0.45 (0.42–0.49)	0.04 (0.02–0.07)
Wildebeest	0.30 (0.21–0.41)	0.04 (0.01–0.12)
Waterbuck	0.49 (0.33–0.65)	0.08 (0.03–0.17)
Giraffe	0.54 (0.49–0.59)	0.07 (0.05–0.10)
Buffalo	0.62 (0.55–0.68)	0.08 (0.04–0.17)

The results presented are the estimates from a logistic regression

Values in parentheses are 95% confidence intervals

Table 4 Probabilities of being involved in an interaction or in a costly interaction when elephants were present (data from 2003)

Species	Number of groups	Interaction	Costly interaction
Impala	153	0.17 (0.12–0.24)	0.08 (0.05–0.14)
Kudu	169	0.19 (0.14–0.26)	0.11 (0.07–0.16)
Roan	63	0.19 (0.11–0.31)	0.08 (0.03–0.18)
Sable	79	0.19 (0.12–0.29)	0.09 (0.04–0.17)
Warthog	138	0.15 (0.10–0.22)	0.03 (0.01–0.07)
Zebra	295	0.20 (0.16–0.25)	0.08 (0.05–0.11)
Wildebeest	24	0.08 (0.02–0.28)	0
Waterbuck	17	0	0
Giraffe	221	0.13 (0.09–0.18)	0.07 (0.04–0.11)
Buffalo	143	0.15 (0.10–0.21)	0.05 (0.02–0.10)

The results presented are the estimates from a logistic regression

Values in parentheses are 95% confidence interval
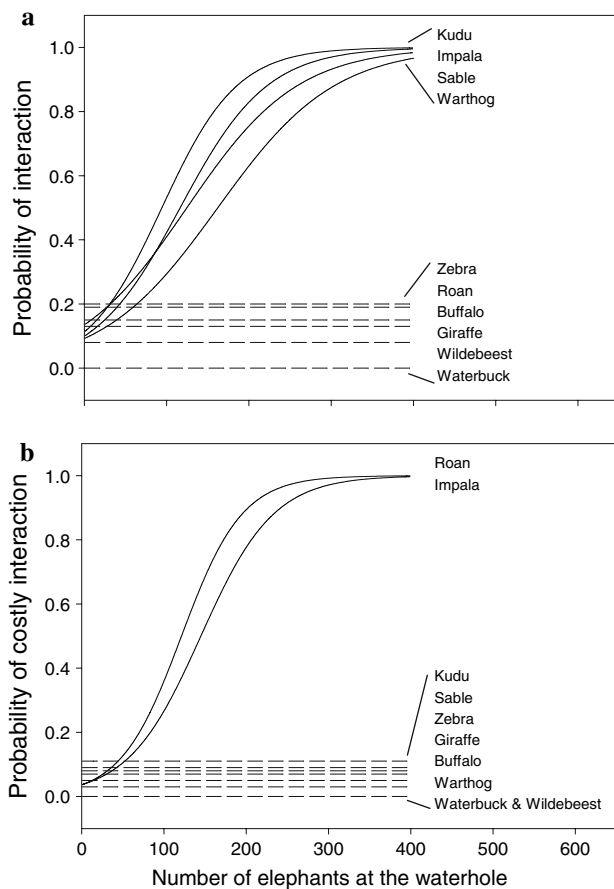
Fig. 3a–b Relationship between the number of elephants at the waterhole and the probability of being involved in **a** any interaction, **b** a costly interaction. Results from logistic regression models (*solid lines* represent significant models with *P* < 0.1 and *dotted lines* represent nonsignificant models with *P* > 0.1)

in the presence of elephants. Most species presented similar probabilities of being involved in an interaction, as well as in a costly interaction (Table 4).

The probability of being involved in an interaction (noncostly or costly) increased significantly with the number of elephants at the waterhole for four species (Fig. 3a; impala: estimate = 0.0189 [95% CI = 0.0085 – 0.0293]; $\chi^2_{(1,151)}$ = 12.65; *P* = 0.0004/kudu: estimate = 0.0219 [95% CI = 0.0098 – 0.0339]; $\chi^2_{(1,167)}$ = 12.58; *P* = 0.0004/ sable: estimate = 0.0149 [95% CI = –0.0016 – 0.0314]; $\chi^2_{(1,77)}$ = 3.14; *P* = 0.0764/warthog: estimate = 0.0141 [95% CI = 0.0045 – 0.0237]; $\chi^2_{(1,136)}$ = 8.3; *P* = 0.004). The probability of being involved in a costly interaction increased significantly with the number of elephants at the waterhole for only two species (Fig. 3b; impala: estimate = 0.0226 [95% CI = 0.0106 – 0.0346]; $\chi^2_{(1,151)}$ = 13.67; *P* = 0.0002/roan: estimate = 0.0271 [95% CI = 0.0045 – 0.0496]; $\chi^2_{(1,61)}$ = 5.54; *P* = 0.0186). The discrepancy between potential and realized risks of interaction (compare Fig. 3 with Table 4) arises because very

few groups arrived at waterholes when many elephants were present and so had a very high probability of being involved in an interaction.

Temporal niche

As shown previously, the average temporal niche of each herbivore species overlapped somewhat with the average temporal niche of elephants, although the degree to which they overlapped differed (Fig. 1). We distinguished two distinct groups of species with regards to arrival times and temporal overlaps: those with a fairly constant mean arrival time at waterholes and with the temporal overlap with elephants increasing with the mean number of elephants (wildebeest, waterbuck, and giraffe), and those for which the mean arrival time changed with the mean arrival time of elephants while the temporal overlap with elephants remained fairly constant (impala, kudu, roan, sable, and buffalo) (Fig. 4). In the latter species, most kept a fairly constant niche breadth; however, roan and sable temporal niches became wider when elephants arrived earlier (roan: $F_{(1,13)}$ = 6.1; *P* = 0.028; r^2 = 0.27; sable: $F_{(1,13)}$ = 6.5; *P* = 0.023; r^2 = 0.28). This indicates that some of the roan and sable groups shifted to earlier temporal niches, whereas others did not.

Discussion

In this paper, we provided one of the first studies on interspecific interference competition in a natural large mammal community. We predicted that species affected by interference competition with elephants would shift their temporal niches at waterholes to avoid high temporal overlap with elephants. Our results provided a coherent picture of animal interactions and behavioral adjustments. They also showed that behavioral adjustments such as temporal niche shifts were successful in maintaining a constant overlap with the competing species. Four species (impala, kudu, roan, and sable) shifted their temporal niches based on elephant activity time and therefore maintained constant temporal overlaps with elephants at waterholes. Interestingly, these four species had higher probabilities of being involved in an interaction with elephants when elephants at the waterhole were numerous. They were also the most likely to suffer from costly interference from elephants. Moreover, the average temporal niches of these four species were the furthest from the elephants'. This strongly suggested that these four species shifted their temporal niches to avoid high temporal overlap and consequently interference competition with elephants. Unexpectedly, buffalo also shifted its temporal niche, although it was not one of the species most likely to
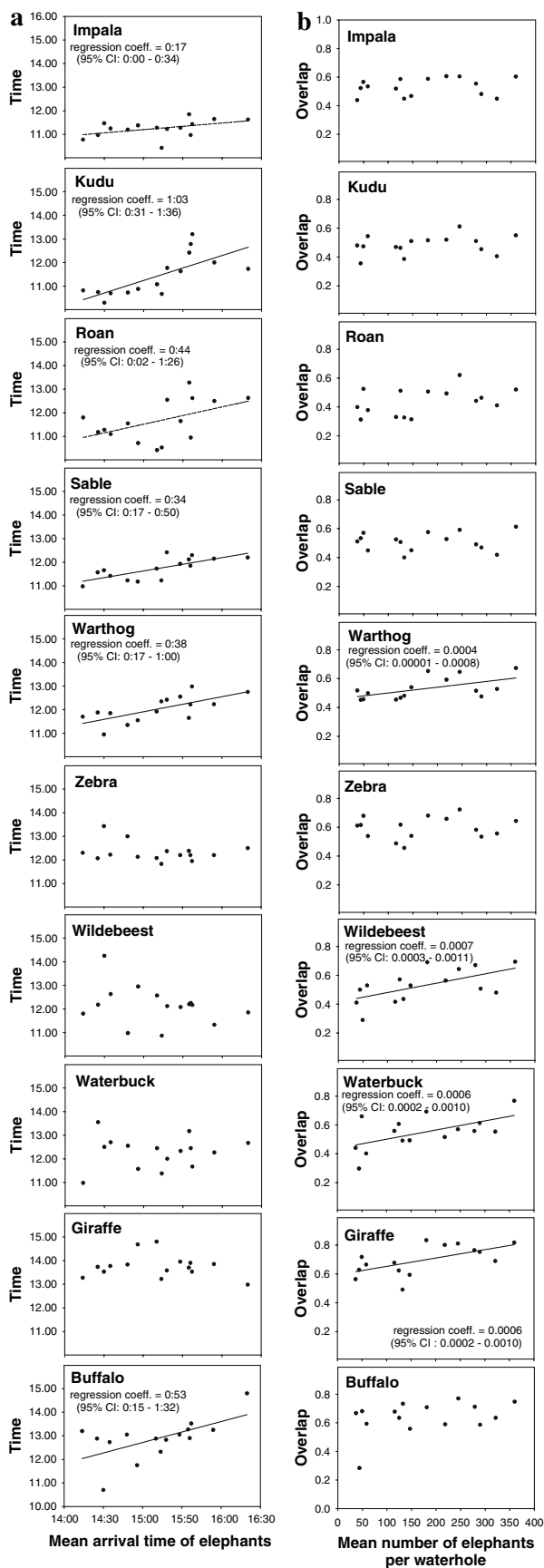
◄ **Fig. 4a–b** **a** Relationship between the mean arrival time of elephants at waterholes and the mean arrival times of various other herbivore species at waterholes. **b** Relationship between the mean number of elephants per waterhole per day and the temporal overlaps of various herbivore species with elephants. Regression lines are displayed when significant (*solid line* when $P < 0.05$ and *dotted line* when $P < 0.1$)

be affected by interference with elephants. This may reflect the need for space at waterholes for large buffalo herds and the fact that elephants are often numerous at waterholes and thus cause congestion. Three species (wildebeest, waterbuck, and giraffe) showed no change in their mean arrival times at waterholes and therefore increased their temporal overlaps with elephants when the mean number of elephants per waterhole increased. Interestingly, these three species were less likely to be affected by interference from elephants than other species and they had a risk of interaction that was independent of the number of elephants at the waterhole. Their average temporal niches also were the closest to the elephants'. Warthog and zebra could be considered to be intermediate species.

To understand why some species are more likely to maintain their time budget and others to change it, and to understand the role that interference competition and induced behavioral adjustments can play in herbivore population dynamics and ultimately in herbivore community structure, there is a need to link our findings with potential fitness costs (Abramsky et al. 2001; Eccard and Ylönen 2002). Species face a tradeoff between the benefits and the costs (e.g., interference competition) of exploiting a shared resource in a given way (see Dickman 1991). In our case, it is the net outcome of the tradeoff between the costs associated with direct interference with elephants and the costs of shifting their temporal niches that will determine the behavioral response of herbivores. This tradeoff is complex to understand because of the variety of potential costs and benefits (predation risk, thermoregulation) and because relating time budgets to costs and benefits is difficult to achieve in the field (Fortin et al. 2004). As species life history traits and characteristics must underlie decisions linked to time budget (du Toit and Yetman 2005), we attempted to identify the characteristics that species that shifted their temporal niches share. We initially focused on water dependency as well as on diets, since grazers are more water-dependent than browsers, and then we focused on body size, which has been proposed to play a role in interaction probability (Palomares and Caro 1999; Loeuille and Loreau 2005) and in predation vulnerability (Sinclair et al. 2003). Surprisingly, we did not find any clear water-dependency-related, diet-related or body-size-related pattern in our results. However, the results in our study are generally consistent with some expected costs of interference competition: time lost from other activities and trav-

eling distances between drinking and feeding sites (Bernstein et al. 1991). Contrary to grassland grazers, whose habitats are often associated with waterhole areas, browsers and woodland grazers cannot forage in the vicinity of waterholes when they fail to drink, and they have to travel between waterholes and woody areas where they forage (Redfern et al. 2003). In dry years, drinking sites as well as foraging patches of acceptable quality are fewer, and this situation induces longer traveling distances and longer times spent searching resources. Consequently, environmental variables influence herbivore time budgets, which end up more constrained in dry years when aggregation around water and associated interference is maximum. If these species have to spend a lot of time attempting to drink, time is therefore lost from other vital activities such as foraging. In our study, it was mainly dry season browsers (impala and kudu) and woodland grazers (roan and sable) that shifted to earlier temporal niches to avoid arriving at waterholes when many elephants might be present, i.e., when the risk of being prevented from drinking was high.

From 1958 to 1960, a similar study on waterhole use by herbivores was carried out in Hwange National Park (Weir and Davison 1965). Sable, roan, kudu, and warthog were species described as using waterholes in the afternoon, with a peak of activity between 14 and 17 h. Nowadays, these species show a peak of activity during late morning (Figs. 1, 4). Therefore, there has been a change in these species' behavior since the late 1950s. In 1960, the elephant population size in Hwange National Park was estimated to 8,000 individuals (Williamson 1975) and elephants used to come to waterholes at night (Weir and Davison 1965), whereas nowadays the elephant population size is estimated to ca. 30,000 individuals (Chamaillé-Jammes 2006) and elephants use waterholes during nighttime and daytime (Figs. 1, 3). Animal behavior has changed in line with the increase in the elephant population, which could suggest that interspecific competition has taken place. The comparison of the two studies reinforces our results. By showing the shift in arrival times at such an important resource in the African landscape, the results from this study provide new insights into the competition between elephants and other herbivore species. This type of information is crucial, as many areas throughout southern Africa have experienced increases in their elephant populations (Blanc et al. 2005). This is the case in Hwange National Park, where most herbivore species have declined over the past 20 years in parallel with the increase in the elephant population, and where questions about the potential competition for water between elephants and other species have arisen (Valeix et al. 2007). One important finding of our study is that the potential costs associated with interference competition at waterholes between ele-

phants and other herbivores are linked to the shifts in activity rather than to the interactions themselves. Because of behavioral adjustments, water acquisition itself is not the ultimate constraint; interference competition at waterholes may instead have indirect costs linked to changes in time budget. If elephant abundance at waterholes leads to a shift in some species' temporal niches and consequently to a redistribution of diurnal activities, the implications of such changes remain poorly understood. The coupling of our findings with research into the costs associated with redistributing diurnal activities will greatly help to optimize water and wildlife management in the future.

In the context of waterhole attendance by herbivores in semiarid savannas, we showed that time represented an important niche axis, over which animals might reduce the effects of interference, as suggested in theoretical studies (Carothers and Jaksic 1984) and demonstrated in previous studies on invertebrates (Loreau 1989; Holway 1999; Albrecht and Gotelli 2001) and small mammals (Kotler et al. 1993; Ziv et al. 1993). This study focused solely on interference competition; exploitation competition was ignored because artificial pumping of water in the dry season keeps a number of waterholes active and maintains them at a given size and therefore reduces depletion of water. However, in more natural systems, the two mechanisms co-occur. As the dry season progresses, evaporation, infiltration as well as depletion of water by animals occur, resulting in water sources becoming scarcer. Consequently, it becomes more difficult and crucial to gain access to surface water. The intensity of the interference relation varies with the extent to which the resource is depleted (Triplet et al. 1999). Consequently, as the water resource becomes depleted, the interference intensifies for this resource. In most natural ecosystems, there will be a need to take into account both interference and exploitation competitive mechanisms. Still, our results strongly suggest that interference competition is a mechanism that is likely to explain temporal partitioning, and that the presence and abundance of behaviorally dominant large species may determine the ecological niches of smaller species to some extent.

References

Abrams PA (1986) Character displacement and niche shift analysed using consumer-resource models of competition. Theor Popul Biol 29:107–160

Abrams PA, Chen X (2002) The evolution of traits affecting resource acquisition and predator vulnerability: character displacement under real and apparent competition. Am Nat 160:692–704

Abramsky Z, Rosenzweig ML, Subach A (2001) The cost of interspecific competition in two gerbil species. J Anim Ecol 70:561–567

Adler FR, Mosquera J (2000) Is space necessary? Interference competition and limits to biodiversity. Ecology 81:3226–3232

Albrecht M, Gotelli NJ (2001) Spatial and temporal niche partitioning in grassland ants. Oecologia 126:134–141

Amarasekare P (2002) Interference competition and species coexistence. Proc R Soc Lond B 269:2541–2550

Berger J, Cunningham C (1998) Behavioural ecology in managed reserves: gender-based asymmetries in interspecific dominance in African elephants and rhinos. Anim Conserv 1:33–38

Bernstein C, Kacelnik A, Krebs JR (1991) Individual decisions and the distribution of predators in a patchy environment. II. The influence of travels costs and structure of the environment. J Anim Ecol 60:205–225

Blanc JJ, Barnes RFW, Craig GC, Douglas-Hamilton I, Dublin HT, Hart JA, Thouless CR (2005) Changes in elephant numbers in major savanna populations in eastern and southern Africa. Pachyderm 38:19–28

Bond WJ (1993) Keystone species. In: Schulze ED, Mooney HA (eds) Biodiversity and ecosystem function. Springer, Berlin, pp 237–253

Bothma JP (1989) Game ranch management. van Schaik Uitgewers, Pretoria

Caro TM, Stoner CJ (2003) The potential for interspecific competition among African carnivores. Biol Conserv 110:67–75

Carothers JH, Jaksic FM (1984) Time as a niche difference: the role of interference competition. Oikos 42:403–406

Case TJ, Gilpin ME (1974) Interference competition and niche theory. Proc Natl Acad Sci USA 71:3073–3077

Chamaillé-Jammes S (2006) Under the African sky: from climatic fluctuations to the regulation of populations, the role of surface-water in the spatio-temporal dynamics of an elephant population. Ph.D. thesis, University of Paris 6, France

Chase JM, Abrams PA, Grover JP, Diehl S, Chesson P, Holt RD, Richards SA, Nisbet RM, Case TJ (2002) The interaction between predation and competition: a review and synthesis. Ecol Lett 5:302–315

Cox DR, Snell EJ (1989) Analysis of binary data. Chapman & Hall, London

Cresswell W (1998) Variation in the strength of interference with resource density in blackbirds, Turdus merula. Oikos 81:152–160

Dickman CR (1991) Mechanisms of competition among insectivorous mammals. Oecologia 85:464–471

Dolman PM (1995) The intensity of interference varies with resource density: evidence from a field study with snow buntings, Plectrophenox nivalis. Oecologia 102:511–514

du Toit JT, Yetman CA (2005) Effects of body size on the diurnal activity budgets of African browsing ruminants. Oecologia 143:317–325

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

Ens BJ, Goss-Custard JD (1984) Interference among oystercatchers, Haematopus ostralegus, feeding on mussels, Mytilus edulis, on the Exe estuary. J Anim Ecol 53:217–231

Fisher NI (1993) Statistical analysis of circular data. Cambridge University Press, Cambridge

Fortin D, Boyce MS, Merrill EH, Fryxell JH (2004) Foraging costs of vigilance in large mammalian herbivores. Oikos 107:172–180

Goss-Custard JD (1980) Competition for food and interference among waders. Ardea 68:31–52

Hanski I (1978) Some comments on the measurement of niche metrics. Ecology 59:168–174

Hardin G (1960) The competitive exclusion principle. Science 131:1292–1297

Holway DA (1999) Competitive mechanisms underlying the displacement of native ants by the invasive argentine ant. Ecology 80:238–251

Kotler BP, Brown JS, Subach A (1993) Mechanisms of species coexistence of optimal foragers: temporal partitioning by two species of sand dune gerbils. Oikos 67:548–556

Loeuille N, Loreau M (2005) Evolutionary emergence of size-structured food webs. Proc Natl Acad Sci USA 102:5761–5766

Loreau M (1989) On testing temporal niche differentiation in carabid beetles. Oecologia 81:89–96

Palomares F, Caro TM (1999) Interspecific killing among mammalian carnivores. Am Nat 153:492–508

Persson L (1985) Asymmetrical competition: are larger animals competitively superior? Am Nat 126:261–266

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Redfern JV, Grant R, Biggs H, Getz W (2003) Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. Ecology 84:2092–2107

SAS Institute Inc. (1999) SAS/STAT software, v8. SAS Institute Inc., Carey, NC

Schoener TW (1968) The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49:704–726

Schoener TW (1983) Field experiments on interspecific competition. Am Nat 122:240–285

Sinclair ARE, Mduma S, Brashares JS (2003) Patterns of predation in a diverse predator–prey system. Nature 425:288–290

Tokeshi M (1999) Species coexistence: ecological and evolutionary perspectives. Blackwell Science, Oxford

Trash I, Theron GK, Bothma JP (1995) Dry season herbivore densities around drinking troughs in the Kruger National Park. J Arid Environ 29:213–219

Triplet P, Stillman RA, Goss-Custard JD (1999) Prey abundance and the strength of interference in a foraging shorebird. J Anim Ecol 68:254–265

Vahl WK, van der Meer J, Weissing FJ, van Dullemen D, Piersma T (2005) The mechanisms of interference competition: two experiments on foraging waders. Behav Ecol 16:845–855

Valeix M, Fritz H, Dubois S, Kanengoni K, Alleaume S, Said S (2007) Vegetation change and herbivore abundance over a period of increasing elephant abundance in Hwange National Park, Zimbabwe. J Trop Ecol 23:87–93

Weir J, Davison E (1965) Daily occurrence of African game animals at waterholes during dry weather. Afr Zool 1:353–368

Williamson BR (1975) Seasonal distribution of elephant in Wankie National Park. Arnoldia 11:1–16

Zar JH (1984) Biostatistical Analysis. Prentice-Hall, London

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