How competition and predation shape patterns of waterhole use by herbivores in arid ecosystems

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Access to surface water is crucial for herbivores in arid ecosystems. Here, we build a game-theoretical model, based on an evolutionary algorithm, to study the influence of ecological factors on the temporal patterns of presence at waterholes in the herbivore community. In this model, we incorporate the specific features of arid environments, namely, the important hydric losses endured by individuals exposed during the warmest hours of the day, and competition for access to water, both within and between species. We also consider the presence of ambushing predators around waterholes, particularly during dark hours. In response to this predation regime, our model predicts a strong aggregative tendency in herbivores. The number of groups, however, is variable, as well as the time these groups choose to attend the waterhole, even if the total number of individuals is fixed. The reason is a multiplicity of possible evolutionarily stable strategies, corresponding to different responses to the trade-off between the advantages of grouping, in terms of risk dilution, and its costs, in terms of increased competition. This variety of possible behavioural responses affects, in turn, the moments when the waterhole is occupied, and the moments when the different species meet each other. In general, herbivores also respond to predation threat by avoiding coming to waterholes after dusk. However, the cumulative effects of a relatively high level of predation during the day and a high level of interspecific competition for access to water may induce an important presence of herbivores at the waterhole at night. Our predictions are discussed in the light of existing empirical studies.

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Because water is a crucial limiting factor in arid and semiarid environments (Gereta, Mwangomo, & Wolanski, 2009; Redfern, Grant, Biggs, & Getz, 2003; Western, 1975), its availability strongly contributes to explaining animal distribution, density and behaviour (Redfern, Grant, Gaylard, & Getz, 2005; Rozen-Rechels et al., 2015; Rueda, Rebollo, Gálvez-Bravo, & Escudero, 2008; Thrash, Theron, Bothma, & Du, 1995). In particular, access to water constrains daily activity patterns and spatial use of the landscape in most herbivore species (Smit, Grant, & Devereux, 2007) and waterholes, as gathering places, concentrate predator—prey interactions (Valeix et al., 2009) and competition among herbivores (Valeix, Fritz, Matsika, Matsvimbo, & Madzikanda, 2007). Competition between herbivore species is often asymmetric, species with large body size generally getting priority over smaller ones (Prins & Olff, 1998).

In addition, the level of competition that prevails around a given waterhole is not constant, because the number of simultaneously present individuals and species vary to a large extent across the day (Valeix, Chamaillé-Jammes, & Fritz, 2007). The conditions encountered by each individual may thus be very different, depending on the time it chooses to attend the waterhole. In this regard, field studies reveal that herbivore species display different preferences for their time of presence at waterholes, and that these preferences also change with ecological conditions (Valeix, 2011; Valeix, Chamaillé-Jammes, et al., 2007).

Time partitioning around a circadian rhythm has indeed been shown to be an effective adaptation to competitive and dangerous environments (for a review, see Kronfeld-Schor & Dayan, 2003). For example, some ant species tend to shift their foraging activity to colder periods of the day in order to avoid conflicts with more aggressive species (Agarwal & Rastogi, 2009) while, in mice, *Mus musculus*, access time to a shared resource may be modified according to the level of aggressiveness displayed by competitors (Howerton & Mench, 2014). Similarly, digger wasps may adapt their provisioning schedule to avoid nest attacks by brood parasites (Polidori, Bevacqua, & Andrietti, 2010). Concerning the specific

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topic of access to water, Crosmary, Valeix, Fritz, Madzikanda, and Côté (2012) found that herbivores respond to predation and hunting constraints by shifting the time they attend water ponds, and Sitters, Heitkönig, Holmgren, and Ojwang (2009) showed that competition within a herbivore guild containing both wild and domestic species leads to a sharing behaviour for forage but a partitioning behaviour for access to water.

The aim of the present study is to get a better understanding of drivers shaping species assemblages at waterholes in large herbivores living in arid areas. We carry out a theoretical investigation, using a game-theoretical approach, since, in the present situation, the success of the individual depends on the interplay between its own strategy, corresponding to the moment it comes to the waterhole, and the moment chosen by the other animals to do so. While an increasing number of simultaneously present individuals logically leads to more difficult access to water for each of them, other important aspects of life in arid areas, concerning the water balance of the herbivores (Loza, Grant, Stuth, & Forbes, 1992) and the varying levels of predation risk around waterholes (Valeix et al., 2009), are also included in our model.

First, we consider the amplitude of temperature variations occurring across the day in arid environments, and its influence on the water balance of the animals, as this is a very important variable in determining patterns of activity (Loza et al., 1992; Valeix, Fritz et al., 2007). This amplitude can indeed be extremely high (from <10 to >30 °C in Southern African savannah, see Fig. 4 in Veenendaal, Kolle, & Lloyd, 2004), and areas surrounding waterholes are generally open and bare, because of intense trampling. Animals present there are therefore exposed to full sunlight (Brits, van Rooyen, & van Rooyen, 2002; see Fig. 1) and individuals choosing to attend waterholes during the warm hours of the day suffer from very high rates of water loss, which must be compensated for by additional drinking (Ayeni, 1977; Finch, 1972; Valeix, Fritz et al., 2007). By contrast, individuals attending waterholes at dawn or sunset will be spared this additional loss (Loza et al., 1992). To incorporate this effect, we assume in the model that animals attending the waterhole during the warmest hours of the day suffer from a reduced drinking efficiency.

The second prominent feature of waterholes is that, as necessary aggregation places for herbivores, they are also among the favourite hunting places for carnivores, and many kills do indeed occur there (Hopcraft, Sinclair, & Packer, 2005; Valeix et al., 2009). As large herbivores in the African savannah are mostly hunted by lions, *Panthera leo* (Owen-Smith & Mills, 2008) whose predation occurs mostly at night (Crosmary et al., 2012; Valeix et al., 2009), all partitioning behaviour inducing a shift in drinking time to the nocturnal period will induce a significant increase in predation risk. Therefore, predation risk, while always high around the waterhole, will be assumed to culminate during dark hours, from dusk to dawn.

The third specific feature of the studied situation is the presence of both inter- and intraspecific competitors at the waterhole, which tends to lower the drinking efficiency of each individual, in variable ways, depending on the size of the pond, the total number of present herbivores and frequent asymmetry in competitive abilities between species (Valeix, Chamaillé-Jammes, et al., 2007). Competition among herbivores can take the form of a simple displacement, whereby an individual evicts another one from its drinking place, or of a real chase (Valeix, Chamaillé-Jammes et al., 2007). In both cases, the outcome is reduced access to water for the displaced individual.

Finally, and for different reasons, individual risk of being preyed upon is not independent of the prevailing level of competition. First, large herbivore herds, being more conspicuous than small ones, may more easily draw attention upon them. The negative effects of competition and predation may thus be cumulative (Connell, 2000). This effect, however, is strongly counterbalanced by the risk dilution effect, whereby prey individuals belonging to large groups actually face less chance of being captured, because predators can only target one prey at a time (Scheel, 1993). Large groups thus confer a net benefit to the individual (Fitzgibbon, 1990). Last, in the present situation, individuals attending crowded waterholes have to spend longer periods there to fulfil their daily hydric needs, because of reduced water accessibility. They are therefore exposed to predation risk for a longer period.

The relationships between thermoregulation, competition, predation and prey grouping strategies are thus complex, and the aim of the present model is to derive evolutionarily stable responses to this complex situation. By doing so, we address specific questions. In particular, we study the influence of competition and predation on the possible temporal segregation between herbivore species. We also ask whether competition may lead some individuals to attend waterholes during the warmest, but safest, hours, or during the coolest, but most dangerous, hours. Finally, a better understanding of these behavioural strategies should provide insight into prey – predator interactions at the population
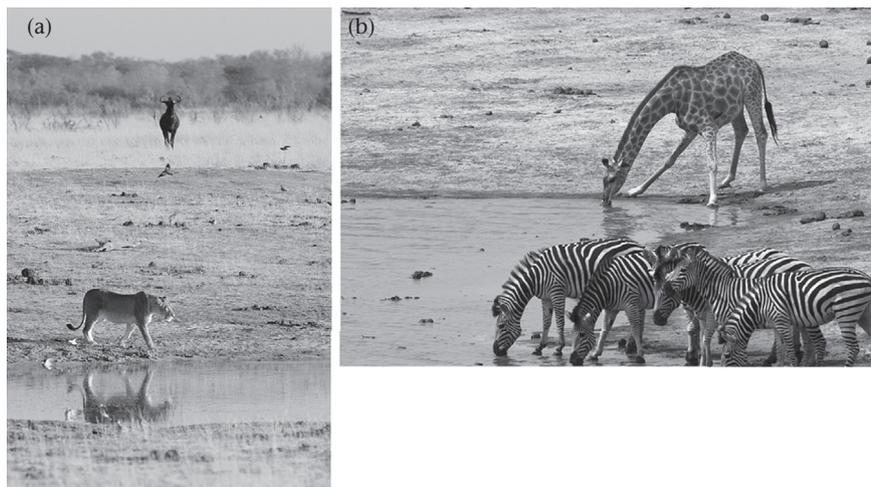

Figure 1. Large mammals attending waterholes in Hwange National Park, Zimbabwe. (a) Lion, *Panthera leo*; (b) zebra, *Equus zebra*, and giraffe, *Giraffa camelopardalis*. Photo: Stéphanie Périquet/CNRS.

level, because the level of risk endured by herbivores affects the dynamics of the whole community (Sinclair, Mduma, & Brashares, 2003).

METHODS: PRINCIPLE OF THE EVOLUTIONARY ALGORITHM

Here we describe how evolutionarily stable patterns of presence at waterholes are derived for a herd of herbivores of given size and composition. The relative complexity of the studied situation, in particular the fact that the strategy within the group will not be described by a single time of arrival, but by a temporal distribution of arrivals whose shape is initially unknown, precludes an analytical approach. For this reason, we make use of an evolutionary algorithm, a numerical method allowing us to identify theoretical endpoints of evolution (i.e. evolutionary equilibria) by simulation of the selective process (Hamblin, 2012). The C++ code is available from the corresponding author.

For modelling purposes, the herd is considered as a closed population. For each of the N herd members, the time of arrival at the waterhole is a fixed strategy, represented by discrete variable x. x can take any value between x_{min} and x_{max}, respectively corresponding to sunrise and sunset. Individuals are allowed to stay at night if they arrive shortly before sunset at the waterhole, but they may not arrive during the night (see Valeix, Chamaillé-Jammes, et al., 2007). Although, in nature, travel from feeding or resting areas to waterholes are also subject to behavioural adaptations, we consider the moment when the animal chooses to arrive at the waterhole as the behavioural trait undergoing selection (see Valeix, Fritz, et al., 2007).

Individuals stay at the waterhole until they have consumed the quantity Q of water they must ingest every day, then leave the waterhole. Each individual present at the waterhole drinks with net rate $D(t)$, which depends on the biology of its species, on the time of day t, and on the number of competitors present. When the individual is not subject to competition, it drinks with maximum net rate $D_{max}(t)$, which also depends on the biology of its species and on the time of day. This net drinking rate incorporates both water intake, through drinking, and water losses, through evaporation. It decreases from sunrise to noon, then increases again from noon to sunset (see Fig. 2), because evaporative water losses are tightly correlated with air temperature (Loza et al., 1992), and air temperature continuously increases, then decreases, over the day (Veenendaal et al., 2004).

In addition, individual drinking rate decreases if the number of individuals present exceeds the capacity C of the waterhole, as a result of space limitation along the waterline (Castelda, Napora, Nasseri, Vyas, & Schulte, 2010). For the sake of simplicity, we do not consider the exact position of the individuals within the group. We simply incorporate density dependence by considering the mean effects of an increasing number of competitors on the success of each individual (see Dolman, 1995).

The waterhole capacity corresponds to the number of individuals that may simultaneously drink without being hindered by one another. If the number of simultaneously present individuals, N_p, does not exceed C, each individual ingests water with maximum rate $D_{max}(t)$. If N_p exceeds C, individual drinking rate decreases as a result of competition for space. It is given by:

$$D(t) = D_{max}(t) \times C/N_p \tag{1}$$

If two species are simultaneously present, with respective abundances $N_{p,1}$ and $N_{p,2}$, one of them (say, species 1) may dominate the other (say, species 2). In this situation, all individuals drink with maximum rate if $N_{p,1} + N_{p,2} \leq C$. Otherwise, the respective individual drinking rates within species 1 and 2 are given by:
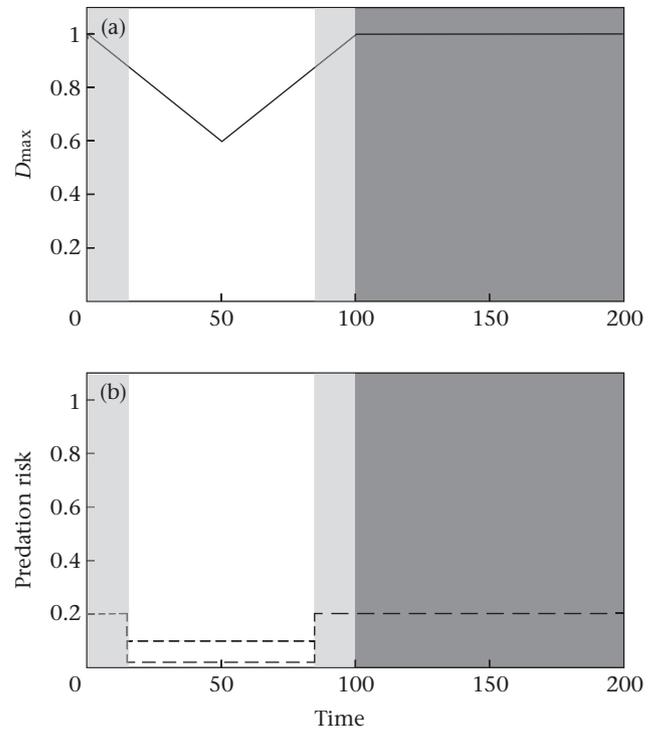

Figure 2. Variation in ecological conditions with circadian time (200 time units = 24 h). The darkest part of the graph corresponds to night and the lightly shaded parts to dawn and dusk. (a) Variation in the net maximum drinking rate, D_{max}, which incorporates both drinking and evaporative water losses. (b) Variation in the basic level of predation risk, P_0, in two types of environment (see text).

$$D_1(t) = D_{max,1}(t) \times p, \text{ and } D_2(t) = D_{max,2}(t) \times p \times \alpha \tag{2}$$

where p denotes the probability of finding a place along the waterline for a member of species 1, and α is the dominance coefficient, which ranges from 0 (total dominance: members of species 2 may drink only if the number of present individuals from species 1 does not exceed the waterhole capacity, i.e. $N_{p,1} < C$) to 1 (no dominance: members of species 1 and 2 have equal access to water). To derive the value of p, we consider that the mean number of simultaneously drinking individuals corresponds to the waterhole capacity, i.e.

$$N_{p,1} \times p + N_{p,2} \times p \times \alpha = C \tag{3}$$

Since conditions vary across the day, the drinking rate of each individual depends on its arrival time. This influences, in turn, the time it has to stay at the waterhole to fulfil its daily needs. To evaluate the benefits of each possible strategy, we use, as a fitness measure, the probability of escaping predators, computed over the whole period spent at the waterhole by the individual. For the sake of simplicity, and in order to take into account the high level of risk prevailing around waterholes, we indeed assume that individuals can be killed only when present there (Valeix et al., 2009).

P_0 denotes the basic probability of a predatory attack, per time unit, on animals present at the waterhole. This basic probability reflects the mean level of threat in the environment. The real probability of an attack may, however, increase with herd size, because large herds are more conspicuous. This probability is then:

$$P_{att} = P_0 \times (N_{p,1} + N_{p,2})^\beta \tag{4}$$

where $\beta \geq 0$ denotes the level of predators' attraction towards large herbivore aggregations. In our derivations, we also consider that

$\beta \leq 1$, because risk dilution generally offsets the higher detectability of large groups (Fitzgibbon, 1990).

Because of risk dilution, the per time unit probability of being killed for a particular individual is finally:

$$P_{killed} = P_{att} \times \gamma / (N_{p,1} + N_{p,2}) \tag{5}$$

where γ denotes the capture probability for the predator.

The probability of being killed is computed in the same way during the day and during the dark hours, except that, due to the nocturnal habits of many predators, the per time unit probability of a predatory attack, P_0, is higher from dusk to dawn. Two types of environments are considered. In the first, this predation risk is decreased by a 10-fold factor during the day, compared to the dark hours. In the second, it is only decreased by a twofold factor (see Fig. 2).

As a starting point for the simulations, we randomly assign a time of arrival x at the waterhole to each of the N individuals, following a uniform distribution between x_{min} and x_{max}. Then, we simulate patterns of arrivals and departures over the day, each individual arriving at the time corresponding to its strategy x, and leaving the waterhole when it has fulfilled its daily hydric needs. At the end of the day, we simulate the selection process by eliminating the 5% of the individuals that have cumulated the lowest probability of surviving predation over the whole period spent at the waterhole. Surviving individuals keep their arrival strategy for the following day, while dead individuals are replaced by new individuals, to keep herd size constant. To each of these new individuals we assign the arrival strategy of a surviving individual from the preceding generation, the probability of choosing a particular surviving individual being proportional to its surviving probability, hence, to its fitness.

Finally, we consider the possible occurrence of mutations. Each of the N individuals has a probability 0.05 of mutating. In this case, it is assigned a new arrival strategy, randomly chosen between x_{min} and x_{max}. This high rate of mutation was chosen to make the appearance of novel strategies possible even in groups of limited size, in order to fully explore the space of possible behaviours (Hamblin, 2012).

This selection − mutation process is reiterated 19 950 times, then mutations are stopped, in order to eliminate the noise inherent in this numerical approach, and, during 50 additional periods, only selection takes place. This large number of iterations was chosen in order to ensure that the resulting equilibria were really stable (see Beauchamp & Ruxton, 2008). The stable distributions we finally get are used to draw the conclusions of the study.

Wide ranges of values were explored for the different parameters, in order to get a global overview of the situation. Although the behavioural strategies we obtain, as a response to the joint influence of both thermoregulatory and predation constraints, depend on the relative strength of each of these factors, distinctive patterns emerge that we present in the Results. In this section, we focus on the influence of varying levels of predation risk during daytime ($P_{0\text{-day}} = 0.02–0.1$), and varying numbers of animals ($N = 30–60$), in either a monospecific herd, or a mixed herd containing equal numbers of individuals from two species. Other parameters are kept constant: $Q = 14$, $C = 20$, $\alpha = 0.05$, $\beta = 0.5$, $\gamma = 1$, $P_{0\text{-dark hours}} = 0.2$.

RESULTS

The first result of our study is that, for any set of conditions, concerning both the composition of the herd and the environment, the evolutionarily stable distribution we obtain may take different shapes. This means that, in the wild, a specific set of conditions may be compatible with different behavioural patterns.

Hereafter, we illustrate this multiplicity by successively presenting the possible responses of a monospecific herd of given size to an increasing level of intraspecific competition, to an increasing level of interspecific competition and to a higher level of predation threat during the day.

Response to Intraspecific Competition

In the case of a monospecific group of limited size, the model predicts a fully aggregative and diurnal pattern of activity. All individuals attend the waterhole simultaneously (Fig. 3a, b), and avoid being present there during dark hours. Although the herd's presence is possible at any time of day, the animals show a preference for the hours that immediately follow dawn (Fig. 3a) or immediately precede dusk (Fig. 3b).

Members of larger herds also display diurnal habits (Fig. 3c–h), and may retain a fully aggregative behaviour. They then come to the waterhole either in the morning (Fig. 3c) or in the afternoon (Fig. 3d). The herd may, however, also split up into two herds of smaller sizes (Fig. 3e–h). Temporal segregation between these two subgroups is then either total (Fig. 3e, f), or partial (Fig. 3g, h). In this last situation, herbivore abundance at the waterhole culminates during the warmest hours of the day, when the two periods of presence overlap (Fig. 3g, h). Note that, in both situations, the numbers of individuals in the subgroups may be equivalent (Fig. 3e, g) or differ (Fig. 3f, h).

Response to Interspecific Competition

We now consider a herd containing equal numbers of individuals from two different herbivore species, in which one species strongly dominates the other.

Again, the model predicts a wide variety of situations (Fig. 4), as both species may now come in either a single wave or two different waves. When both come in a single wave, the dominants either come in the morning (Fig. 4a) or in the afternoon (Fig. 4b), and the subordinates are then forced to prolong their presence during the warmest hours of the day. It is also possible that the dominant species splits up into two groups, while the subordinate retains a fully gregarious behaviour (Fig. 4c).

The opposite situation, where only the subordinate species splits up, is also possible (Fig. 4d). One group of subordinates is then spared from interspecific competition, while the other, albeit of smaller size, has to stay longer at the waterhole because of the presence of the whole herd of dominants (Fig. 4d). Note that the second group of the subordinate species responds to this presence by slightly extending its presence at dusk (Fig. 4d).

Finally, both species may split up (Fig. 4e). The presence of the dominant species at the waterhole is then discontinuous, while, in the subordinate species, the times the groups are present overlap during the warm hours of the day (Fig. 4e).

Response to an Increased Predation Risk during the Day

If predation risk during the day is increased, the diurnal patterns described in the preceding situation are still possible (see Fig. 4). However, new types of situations may also be encountered, where one or both species exhibit partly nocturnal habits. The subordinate species may indeed now respond to the presence of the dominant during the coolest hours of the day by extending its presence well after dusk (Fig. 5a). Moreover, the dominants may also extend their presence during the dark hours. The subordinates respond by
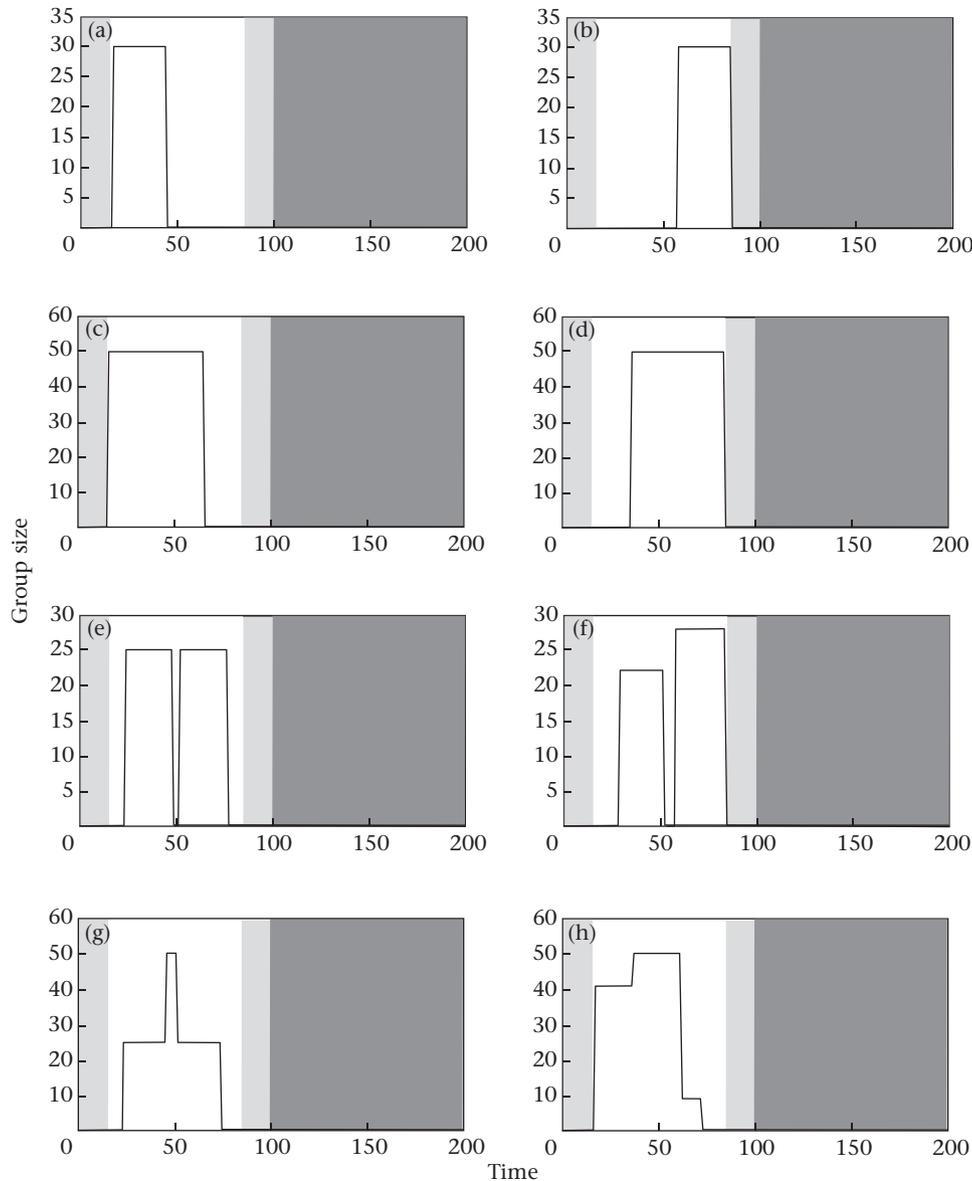
Figure 3. Monospecific group: the number of individuals present at the waterhole as a function of time. Total herd size: (a, b) $N = 30$; (c–h) $N = 50$. Other parameter values: $Q = 14$, $C = 20$, $\beta = 0.5$, $\gamma = 1$, $P_{0\text{-day}} = 0.02$, $P_{0\text{-dark hours}} = 0.2$. (a, b and c–h) Different types of patterns obtained for a similar set of parameter values.

staying at the waterhole for a relatively long time after nightfall (Fig. 5b).

DISCUSSION

Our model shows that temporal patterns of waterhole use by herbivores during the day can encompass a variety of strategies, even when the size and composition of the whole herd are fixed. The primary explanation dwells in the strong Allee effect deriving from risk dilution within groups of prey. As a consequence of this effect, if herbivores tend to aggregate at the waterhole at certain times of day, an individual choosing not to join any of these groups endures tremendous predation risk, and its strategy can then not endure. This is why aggregative patterns of presence at the waterhole become evolutionarily stable strategies, even if the time chosen to attend the waterhole is suboptimal for the group. In fact, the advantages of associating with others make the present game a

coordination game, and multiple equilibria are the rule for this kind of game (e.g. Brosnan, Wilson, & Beran, 2012).

Nevertheless, and even though our model strictly considers individual decisions, the different types of distributions we obtain reflect different types of collective response to the trade-off encountered in the wild, between the advantages of group living and the reduced access to water endured in large herds. Herbivores may indeed favour either a greater level of risk dilution by attending a large group, even if this increases the total time they have to stay at the waterhole (e.g. Fig. 3c, d), or a lesser level of competition for water, by coming in two successive waves, which exposes them for shorter times, but with a lower level of risk dilution (e.g. Fig. 3e, f). An intermediate situation, where a given individual successively encounters both types of conditions, is also possible, as the times of presence of the different groups may partly overlap (e.g. Fig. 3g, h). Adaptive patterns of presence at the waterhole are thus compatible with different types of social organization.
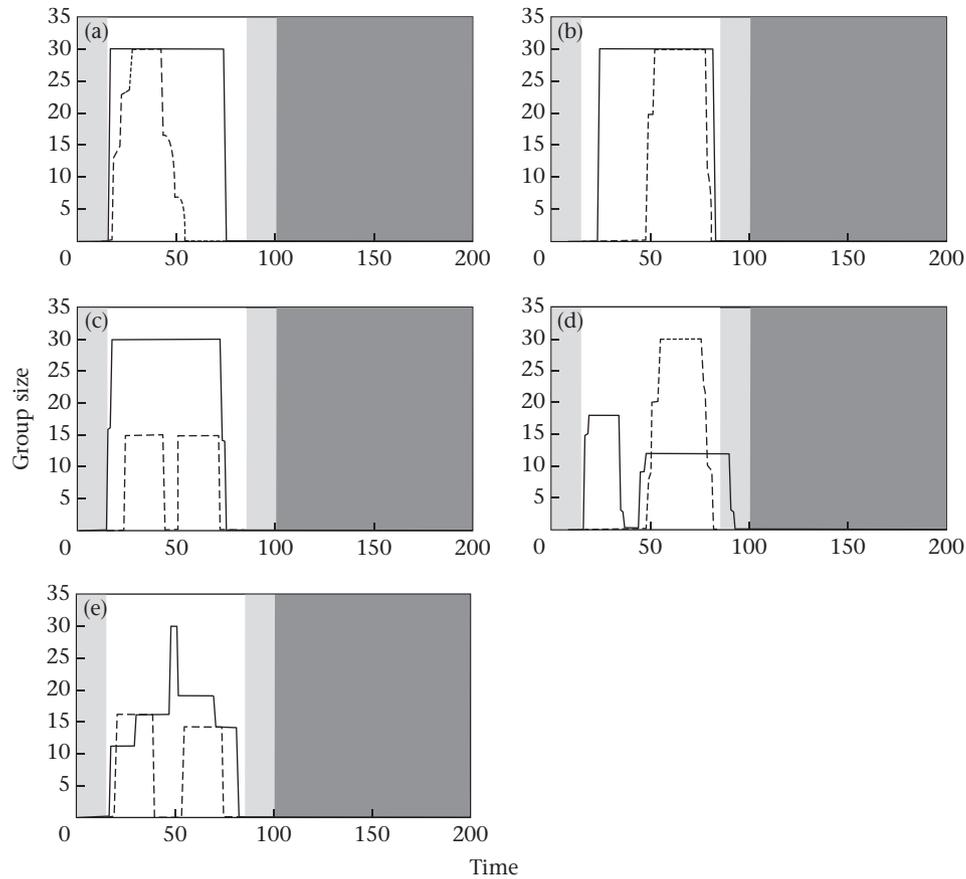
Figure 4. Mixed group with asymmetric competition: the number of individuals present at the waterhole as a function of time. The full line corresponds to the subordinate species, the dashed line to the dominant species. Total herd sizes: $N_1 = N_2 = 30$. Other parameter values: $Q = 14$, $C = 20$, $\beta = 0.5$, $\gamma = 1$, $\alpha = 0.05$, $P_{0\text{-day}} = 0.02$, $P_{0\text{-dark hours}} = 0.2$. (a—e) Different types of patterns obtained for a similar set of parameter values.
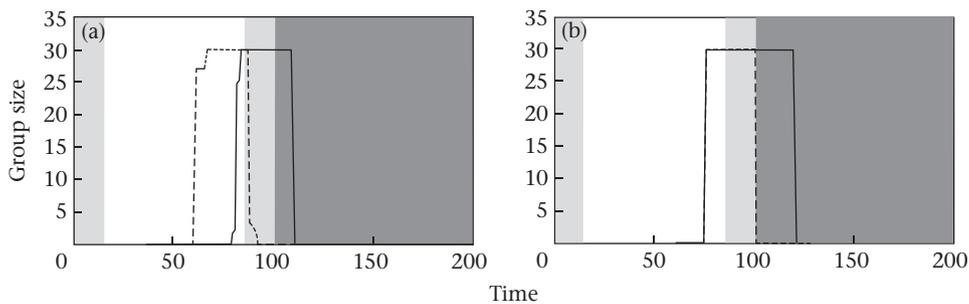

Figure 5. Response to an increased predation risk during the day: the number of individuals present at the waterhole as a function of time. The full line corresponds to the subordinate species, the dashed line to the dominant species. Total herd sizes: $N_1 = N_2 = 30$. Other parameter values: $Q = 14$, $C = 20$, $\beta = 0.5$, $\gamma = 1$, $\alpha = 0.05$, $P_{0\text{-day}} = 0.1$, $P_{0\text{-dark hours}} = 0.2$. (a, b) Different types of patterns obtained for a similar set of parameter values.

When animals come in several groups, evolutionary stability is achieved by success equalization between groups, and the spreading of arrivals coincides with a temporal ideal free distribution (Iwasa & Levin, 1995). The situation may nevertheless differ between groups, because conditions around the waterhole vary across the day. Thus, when groups vary in size, fitness equalization is possible for two different reasons. First, the advantages associated with risk dilution tend to compensate for the longer time that the larger group has to stay at the waterhole. Second, one group may attend the waterhole during warmer hours than the other, which also influences total presence time for this group (e.g. Fig. 3f and h). Asymmetry in group size hence coincides with asymmetric

temporal patterns of presence, with respect to the middle of the day (compare Fig. 3f, h with Fig. 3e, g).

The trade-off between the advantages and drawbacks of living in a large group is also present in the case of a mixed herd, but the response to another species' presence is expected to vary between a dominant and a subordinate species. The cost of associating with heterospecifics is indeed much heavier for members of the subordinate species than for members of the dominant species, while the level of dilution risk is the same for all individuals. It is thus advantageous for dominants to be present at the same time as subordinates, while subordinates should avoid being present at the same time as a large herd of dominants. The final mixed

distribution should then be interpreted as a coevolutionary equilibrium between competing species.

Here again, different types of situations are possible, ranging from the case where both species come in a single wave (Fig. 4a, b), to the case where both split up into smaller groups (Fig. 4e). When the whole group of subordinates is present, the dominant species may either come as a single group (Fig. 4a, b), or split up (Fig. 4c), which was not possible when subordinates were absent (see Fig. 3a, b). The density threshold above which splitting is possible thus decreases for the dominant species when subordinates are present.

When at least one species arrives at the waterhole in two separate waves, the results must once more be interpreted in the light of ideal free distribution theory. For example, members of the subordinate species may come in two separate groups that endure very different conditions. The first, spared from interspecific competition, stays for a relatively short time at the waterhole, while the other, accompanied by the whole group of dominants, has to stay much longer, but enjoys a high level of risk dilution (Fig. 4d). The splitting of both species is also possible, and finally yields mixed subgroups of relatively equal sizes (Fig. 4e).

The joint effects of predation and competition on the structure of herbivore communities have been recognized for a long time (Sinclair, 1985). Moreover, social organization within herbivore populations relies on grouping strategies that are, to a large extent, influenced by the two conflicting pressures we considered in our study, namely, risk dilution and competition for access to resources (Sinclair, 1985). Concerning the specific topic of presence at waterholes, where both predation and competition may be high, variable species assemblages have been reported across the day, in accordance with the main prediction of our study (Valeix, Chamaillé-Jammes, et al., 2007). While all species, except elephants, *Loxodonta africana*, generally avoid being present at night, members of most species exhibit preferences for specific moments of the day, such as midmorning, mid-afternoon or midday, and bimodal patterns of presence, with presence in both the morning and the afternoon, are also possible (Valeix, Chamaillé-Jammes, et al., 2007).

Our model shows that, even if coming to the waterhole in the middle of the day is costly from a thermoregulatory point of view, adaptive grouping strategies, as a response to predation risk, may nevertheless lead animals to be present in high numbers during the warmest hours of the day (see Figs. 3g, h, 4). This pattern has often been reported in the field (e.g. Valeix, Chamaillé-Jammes, et al., 2007).

Dominance between species is most of the time ruled by differences in size (Prins & Olff, 1998), large species evicting smaller ones from drinking places, either passively or after attacking them (Valeix, Chamaillé-Jammes, et al., 2007). As a response to an increasing presence of interspecific competitors, subordinate species may then decide to shift their arrival time at the waterhole, even if they endure additional thermoregulatory costs. This behavioural response has been demonstrated in several ungulate species dominated by elephants, and subject to intense competition when the dry season leads elephants to spend more time at the waterhole (Valeix, Chamaillé-Jammes, et al., 2007). It is also predicted by our model (compare Fig. 3b with Fig. 4b).

While ungulates in arid areas generally attend waterholes only in full daylight (Valeix, Chamaillé-Jammes, et al., 2007), presence at dusk or night is also possible, and empirical evidence suggests that predation is a major driver of such possible nocturnal tendencies. Studying the temporal use of waterholes in nine herbivore species, Valeix et al. (2009) have indeed shown that both the preferred prey of lions (buffalo, kudu and giraffe) and other herbivore species (except warthog) tend much more to avoid visiting a particular waterhole at night when a lion's presence in the vicinity is confirmed. However, even when a lion is present, several prey species also take the risk to visit the waterhole during the dark hours, even if they do not spend long periods there (for instance buffalo, giraffe, impala, roan, kudu, zebra; see Fig. 3 in Valeix et al., 2009). Our study suggests that strong interspecific competition may lead individuals to attend waterholes during the most dangerous hours, which could explain this pattern. This tendency is expected to be strongest in subordinate species, but the arms race between competing species may also lead a dominant species to do so, because the presence of the subordinates confers protection (see Fig. 5b).

Additionally, Crosmary et al. (2012) have shown that, if an ungulate community becomes subject to a high hunting pressure imposed by humans during the day, the animals will change their habits, and begin to regularly visit the waterhole at night, even if natural predation still mostly happens then. These results confirm that the time chosen by the animals to attend a waterhole may be subject to important behavioural plasticity, which is the major assumption of our model. They are also in accordance with our predictions (see Fig. 5).

Confronting real data with our theoretical predictions, however, deserves more scrutiny. It could thus be particularly interesting to focus on the exact length of periods of presence at waterholes, to see if peaks of presence at certain times of the day result from massive arrivals, or, as our model proposes, from a partial overlap between the periods of presence of successive groups.

From a modelling point of view, several specific points could be included, such as the possibility for herbivores to also modulate their behaviour while travelling to the waterhole (Valeix, Fritz, et al., 2007) or their vigilance behaviour while present at the waterhole, in response to varying environmental conditions (Périquet et al., 2010). Nevertheless, the behavioural mechanisms we propose, through our game-theoretical approach, are already bound to influence coexistence rules within herbivore communities in arid ecosystems.

Acknowledgments

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