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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.

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

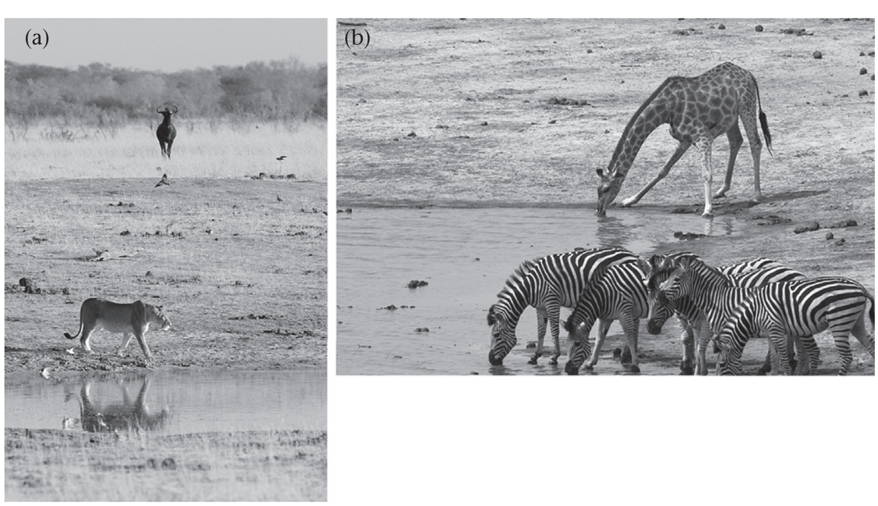

Figure 1. Large mammals attending waterholes in Hwange National Park, Zimbabwe. (a) Lion, *Panthera leo*; (b) zebra, *Equus zebra*, and giraffe, *Giraffa camelopardalis*. Photo: Stéphanie Périquet/CNRS.