

## Water provisioning shapes carnivore community structure

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### Abstract

Water provisioning is common in arid and semi-arid African ecosystems, but its effects on carnivore communities are not understood. Recently, Morin *et al.* documented the unexpectedly contrasting space-use patterns of dominant and subordinate carnivores around water sources, with dominant carnivores facilitating subordinate carnivores.

**Keywords:** water availability; interspecific interactions; carnivore ecology

### Water provisioning in African savannas

Much of southern Africa comprises arid or semi-arid landscapes with variable rainfall [1] and water availability, limiting the distribution of both humans and many wildlife species, especially during dry periods. Besides maintaining wildlife populations for conservation, intact ecosystems with their large charismatic fauna are needed for ecosystem services and economic sustainability through ecotourism and hunting [2]. However, many of these wildlife populations are fenced in or surrounded by human development or agriculture [3], limiting their ability to find water during dry periods.

Water provisioning has become an important wildlife management tool for maintaining wildlife populations in areas deficient in perennial water sources, with water provisioning through natural or artificial waterholes, boreholes, or cattle troughs being common throughout southern Africa [4]. However, the inability of animals to move freely may become progressively more important as climate change causes rainfall variability and increasing extreme weather events, with the resultant reduction in available water being a critical concern for southern Africa [5].

Water provisioning in African protected areas has a long history, and some work has been done on its effects on the ecology of ungulates [4]. Conversely, although some data are available on the activity patterns of carnivores (e.g., [6]), there are limited published data on the implications for carnivore community structure [7]. Hwange National Park in Zimbabwe and Kruger National Park in South Africa have been providing water since the 1930s [4]. This was done initially not to mitigate climate change but to provide game with year-round access to water, increase their numbers, and allow for a more even distribution across the landscape, improving sightings for tourists. By 1980, Kruger National Park had around 300 artificial waterholes, with most wildlife recorded within 5 km of a water source, thus creating the desired effects, which were, at the time, seen as wholly positive [4].

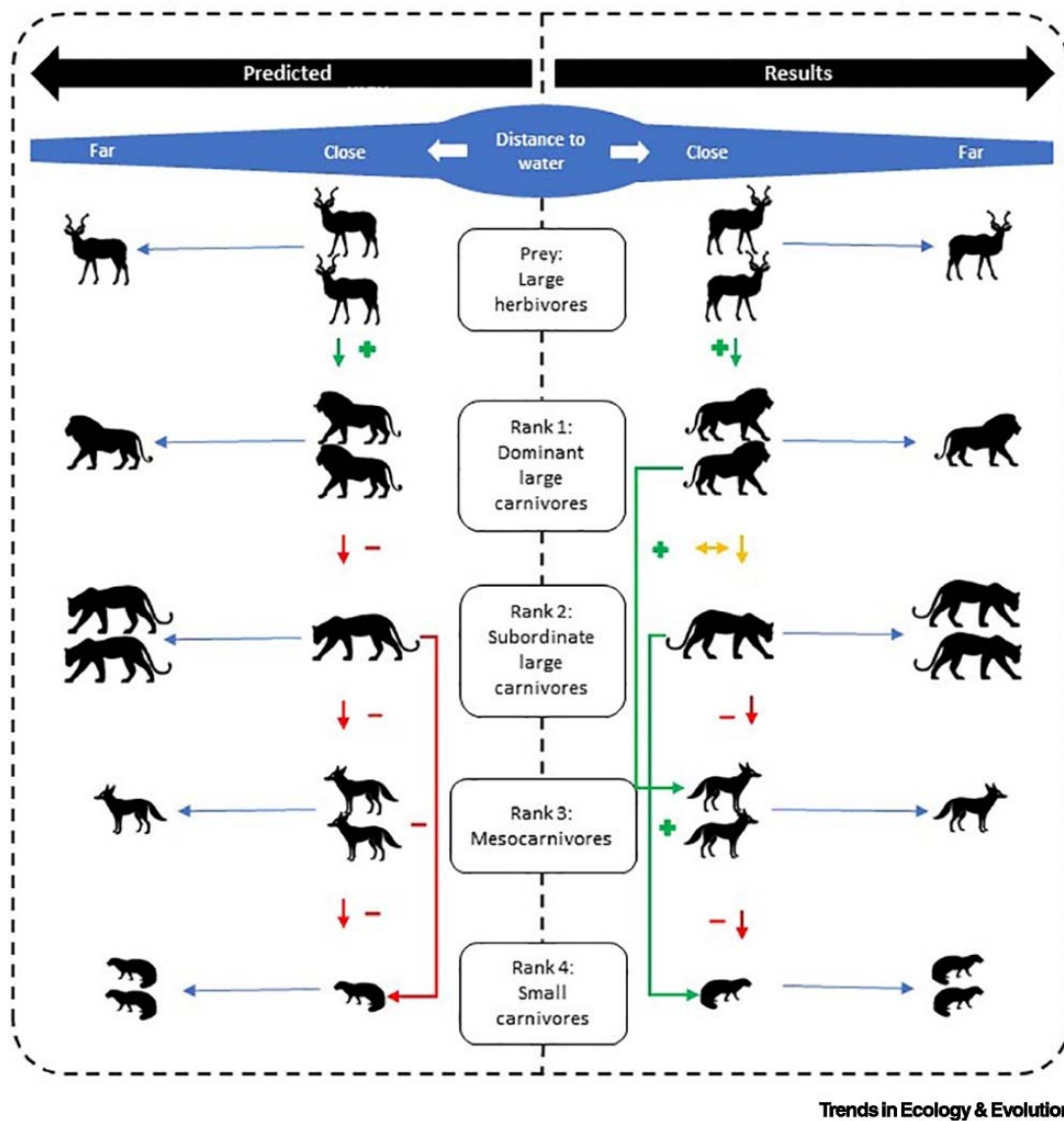
However, there were numerous negative impacts, including trampling and a reduction in vegetation surrounding the waterholes [8], and temporal and spatial changes in certain species interactions. In Hwange National Park, increased water led to an increase in elephant (*Loxodonta africana*) numbers [9]. Elephants around waterholes changed the activity patterns of certain smaller species, leading to a change in diurnal activity among herbivores [10]. A particularly important impact of artificial water provisioning in Kruger National Park was the decline in the rare roan antelope (*Hippotragus equinus*), resulting from increases in blue wildebeest (*Connochaetes taurinus*) and common zebra (*Equus quagga*), and this prey base supporting the subsequent increase in lion populations [11]. This effect was used as an important motivation for initiating the closing of waterholes in 1994 [11].

In terms of carnivore communities, only Edwards *et al.* [7], through their work in the Namib Desert, have analyzed the effects of water availability and found that carnivores largely use temporal partitioning, but also spatial partitioning at water resources to avoid competition. Species showing greater differences in body mass displayed greater spatial partitioning at water sources, possibly reducing direct encounters. This is the expected trend, and supports the notion that artificial water provisioning is detrimental to smaller carnivore species [6].

### **Effects of water provisioning on carnivore community structure**

By contrast, Morin *et al.* [12] recently showed that this body size-based dominance hierarchy is not a hard rule. Their findings are novel and show how artificial water provisioning shapes the structure of, and interactions within, an African carnivore community in Hwange National Park. The authors used camera traps to collect data on the carnivore community at various distances from water. Instead of investigating the effects of water on individual species, they considered impacts on functional groups. They grouped the carnivores into four ranks based primarily on body size: Rank 1 included dominant large carnivores [lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*)]; Rank 2 included the subordinate large carnivores [leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), brown hyenas (*Hyaena brunnea*), and African wild dogs (*Lycaon pictus*)]; Rank 3 included the mesocarnivores [caracal (*Caracal caracal*), black-backed jackals (*Lupulella mesomelas*), side-striped jackals (*Lupulella adustus*), servals (*Leptailurus serval*), African civets (*Civettictis civetta*), honey badgers (*Mellivora capensis*), and aardwolf (*Proteles cristata*)]; and finally, Rank 4 constituted the small carnivores [African wild cats (*Felis lybica*), bat-eared foxes (*Otocyon megalotis*), striped polecats (*Ictonyx striatus*), and all the mongoose and genet species].

Their key finding was that water availability had differential impacts on the spatial distribution of these functional groups (Figure 1), altering the structure of the carnivore community. Close to waterholes, dominant large carnivores (Rank 1) displayed the highest probability of occupancy, followed by mesocarnivores (Rank 3). By contrast, subordinate large carnivores (Rank 2) and small carnivores (Rank 4) were less likely to occur in these areas (Figure 1). This pattern suggests possible spatial avoidance between adjacent ranks, in contrast to the expected result of a hierarchy from the largest dominant species to the smallest.



**Figure 1. The predicted and unexpected observed effects of distance to water on carnivore community structure.** Large dominant carnivores (Rank 1) and mesocarnivores (Rank 3) had higher occupancies near water. By contrast, large subordinate carnivores (Rank 2) and small carnivores (Rank 4) had lower occupancies in these areas, suggesting that they avoided them. Green '+' signs indicate an increase in occupancy. Red '-' signs denote a decrease. Bidirectional yellow arrows suggest spatial overlap with neutral or minimal competition between adjacent ranks.

Interestingly, although Rank 2 overall occupancy decreased near water, Rank 1 positively influenced their conditional occupancy. This means that, when Rank 1 species were present, Rank 2 species were more likely to be detected. This suggests that Rank 2 species were affected by competition but could still use the area when the dominant species were present, possibly benefiting from the conditions created.

Surprisingly, the presence of higher ranked carnivores positively affected specific subordinate ranks, regardless of distance to water. This contrasts with the common assumption that dominant carnivores suppress subordinates through interference competition and intraguild predation [3]. The authors proposed that positive interactions, such as carrion provisioning,

could explain this pattern, with subordinate carnivores benefiting from scavenging opportunities despite the risks.

The activity patterns of the ranks in relation to each other had high overlap [12]. However, some subtle shifts in peak activity were observed for subordinate groups. These differences occurred in both high and low water availability areas, suggesting they were not driven by water distribution. However, temporal avoidance may still facilitate carnivore coexistence, but at finer scales not captured by this study.

This study highlights the value of adopting a functional, multispecies approach to understanding community responses to environmental factors. While responses may vary among individual species, the rank-level patterns identified provide novel and unexpected insights into carnivore community dynamics.

### **Conservation implications**

The results of this work have implications for conservation management. Understanding how resources influence community structure is becoming ever more crucial considering the predicted effects of climate change and anthropogenic pressures on carnivores. The study suggests that managers should maintain habitat/landscape variability with respect to distance to water to promote and maintain a higher functional diversity of carnivores. Ensuring that some areas are at greater distances from waterholes may benefit subordinate large carnivores, such as cheetahs and African wild dogs, as well as small carnivores.

### **Data gaps**

The analytical approach used (functional ranks instead of individual species) may obscure certain species-specific behaviors. This is acknowledged by Morin *et al.* [12], who rightly suggest that the work should also be done on a species level. In addition, the absence of prey data for all rank categories, such as rodent and insect availability, and limitations in temporal data regarding other environmental pressures, prevent a complete understanding of occupancy and activity patterns. Despite these potential shortcomings, the authors provide novel information about carnivore community dynamics, finding they are more complex than previously thought.

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### **Declaration of interests**

The authors declare no competing interests.

### **Declaration of generative AI and AI-assisted technologies in the writing process**

During the preparation of this work, the authors used Grammarly to check and correct spelling and grammar. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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