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## Research Report

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# Refuges in time: temporal avoidance of interference competition in endangered wild dogs *Lycaon pictus*

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## Abstract

Competitive interactions can be an important ecological factor in shaping species composition and abundance, with resulting implications for the conservation of inferior competitors. Endangered African wild dogs *Lycaon pictus* are known to suffer from interference competition with lions *Panthera leo* and spotted hyaenas *Crocuta crocuta*. Wild dogs have previously been shown to avoid areas frequented by superior intraguild competitors. Here, we tested the hypothesis that wild dogs

also avoid lions and spotted hyaenas in time. To this end, daily activity patterns of sympatric social groups of the three species were recorded simultaneously by multiple observers in Hluhluwe-iMfolozi Park, South Africa. Wild dogs showed significantly different daily activity patterns compared to lions and spotted hyaenas, suggesting temporal niche separation. Our results raise the question whether conserving competing predators in small fenced conservation areas will lead to management-induced niche shifts.

## Introduction

The recent shift in emphasis from single species to ecosystem conservation is revealing how interactions between species can influence single species viability. Among mammalian carnivores, interspecific competition was found to be an important ecological factor in shaping species composition and abundance (Palomares and Caro 1999; Linnell and Strand 2000; Creel et al. 2001; Caro and Stoner 2003; Donadio and Buskirk 2006). These reviews suggest that interference competition, such as intraguild predation and kleptoparasitism at carcasses, potentially has more serious consequences on population dynamics than exploitation competition, particularly when prey is not a limiting resource. This can have strong implications for the conservation of endangered species that are inferior competitors. For example, cheetahs *Acinonyx jubatus* were shown to suffer from interference competition with lions *Panthera leo* and spotted hyaenas *Crocuta crocuta* and to avoid competitive interactions by retreating to refuge habitats (Durant 1998).

African wild dogs, classified as Endangered by the IUCN (Woodroffe et al. 2004) face similar challenges. Wild dogs throughout their range in sub-Saharan Africa occur at considerably lower densities than sympatric lions and spotted hyaenas, with a negative relationship between the density of wild dogs and densities of lions and spotted hyaenas reported across study sites (Creel and Creel 1996, 1998, 2002). Even within study sites, wild dogs were found to occur at lower density where lions are more abundant (Mills and Gorman 1997; Creel and Creel 2002). Lions predate on wild dogs and exclude them from rich foraging patches (Mills and Biggs 1993; Van Heerden et al. 1995; Creel and Creel 1996, 1998, 2002; Mills and Gorman 1997; Van Dyk and Slotow 2003), whereas spotted hyaenas negatively affect wild dogs mainly by stealing food (Fanshawe and FitzGibbon 1993; Fuller et al. 1995; Creel and Creel 1996, 1998, 2002; Carbone et al. 1997, 2005; Gorman et al. 1998). These factors can reduce foraging efficiency and increase mortality rates and thus may have profound consequences on the population dynamics of wild dogs.

Nevertheless, wild dogs do manage to co-exist alongside lions and spotted hyaenas in most areas, so how then – at the proximate level – do wild dogs avoid competition with sympatric large carnivores? Surprisingly, this question has received little attention to date, not just in wild dogs but for carnivores in general. In the context of interference competition, the additional dimension of niche separation most likely is time (Linnell and Strand 2000), but clear temporal segregation has rarely been found in studies of resource partitioning between sympatric, potentially competing carnivores (Palomares and Caro 1999). Therefore, the aim of this study was to test the hypothesis that wild dogs avoid intraguild interference interactions not only in space but also in time.

## Methods

### *Study area*

Field work was conducted in Hluhluwe-iMfolozi Park (HiP), which is approximately 900km<sup>2</sup> in size and is located in northern KwaZulu-Natal Province, eastern South Africa. The park, with its subtropical climate, has a diverse topography and the predominant vegetation is bushveld savannah. Wild dogs were re-introduced into HiP in 1980/1981 after an absence of half a century (Maddock 1995, 1999; Gusset et al. 2006a; also see Andreka et al. 1999; Krüger et al. 1999; Graf et al. 2006; Gusset et al. 2006b). HiP supports a large potential prey base and a broad spectrum of large carnivores, including lions and spotted hyaenas as potential intraguild competitors of wild dogs. The park is enclosed by an electrified fence.

### *Data collection and analysis*

To assess potential temporal avoidance of competitive interactions, a wild dog pack was selected whose range was known to spatially overlap with a lion pride and a spotted hyaena clan. In each sympatric social group, there was one radio-collared adult female whose activity was monitored remotely. Activity was determined from motion sensors incorporated in the radio collars and treated as a dichotomous variable: active or inactive. Intensive radio tracking periods were conducted over nine consecutive days in April 2005 for four

hours in the early morning (05:00–09:00hrs) and again in the late afternoon (15:00–19:00hrs), during which activity was recorded in ten-minute intervals simultaneously for all three species by multiple observers. For analysis, time spent radio tracking was divided into eight one-hour periods and percentage activity per hour calculated for each species. Finally, daily activity patterns of the three species were overlapped and statistically compared using one-way repeated measures analysis of variance. The statistical test was two-tailed, with the significance level set at  $P = 0.05$ , and was run on Systat 10 (2000).

## Results

The number of activity readings obtained per species was 213, 216 and 234 for wild dogs, lions and spotted hyaenas, respectively. Wild dogs were found to be most active in the early morning and late afternoon. Before sunrise and after nightfall, wild dogs were less active, which were the two periods of the day when lions and spotted hyaenas were more active (Figure 1). The daily activity patterns of lions and spotted hyaenas were analogous and sequentially dissimilar from wild dogs ( $df = 2$ ,  $F = 5.36$ ,  $P = 0.02$ ). The same bimodal pattern of daily activity for wild dogs in HiP was recorded over year-round full-day observational periods (Andreka 1996; pers. obs.).

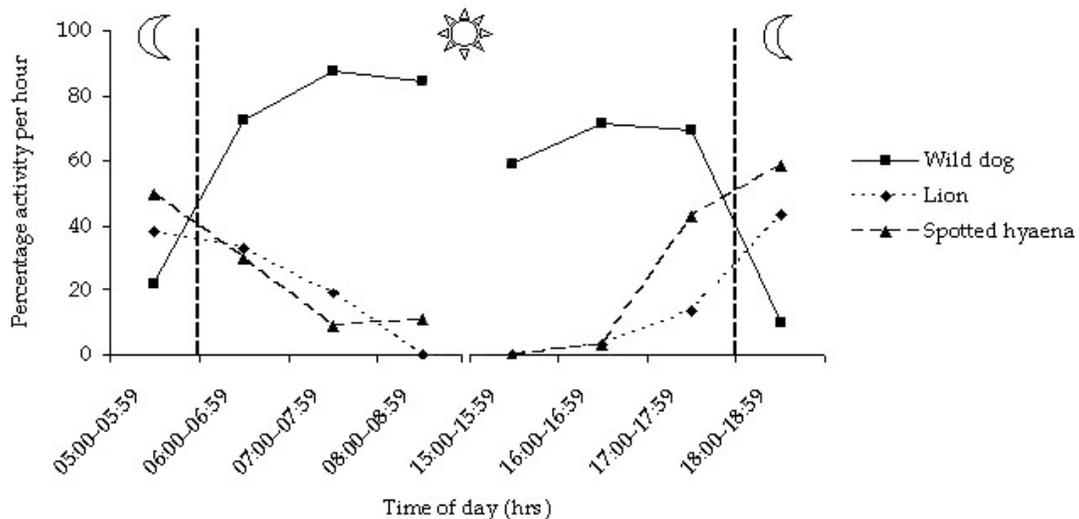


Figure 1. Daily activity patterns of wild dogs, lions and spotted hyaenas in Hluhluwe-iMfolozi Park, showing how wild dogs avoid interference competition in time. Vertical dashed lines indicate sunrise and sunset.

## Discussion

Wild dogs showed significantly different daily activity patterns compared to lions and spotted hyaenas. Although sample size is small, our findings are consistent with the hypothesis that wild dogs avoid interference competition in time. One could argue, however, that wild dogs are excluded from hunting during the night by superior competitors, just as wild dogs are excluded from rich foraging patches (Mills and Gorman 1997; Creel and Creel 2002). This does not seem to be the case, as

wild dogs are highly successful hunters adapted to hunting during daylight (Fuller and Kat 1990; Mills and Biggs 1993; Creel and Creel 2002) and – although known to hunt during moonlit nights – wild dogs do not become nocturnal in areas with low interspecific competition (A. Pole, pers. comm.). It could still be that daily activity patterns differ due to evolutionary adaptations unrelated to intra-guild competition, but the available evidence indicates that temporal niche separation indeed helps wild dogs to co-exist with their superior competitors.

Creel and Creel (1996, 2002) suggested that wild dogs are a fugitive species and range over extremely vast tracts of land compared to lions and spotted hyaenas as an adaptation to finding patches unoccupied by these superior competitors. In small fenced conservation areas, however, retreating to refuge habitats might not be possible (Creel 2001), so one could expect temporal avoidance to be a strong factor in promoting niche separation among sympatric carnivores under these conditions. It remains to be seen if conserving competing predators in confined systems exceeds their behavioural adaptability to potentially stronger competition, with consequently the disappearance of the inferior competitor, or whether they will increasingly segregate in time or another niche dimension. The latter scenario would lead to a phenomenon that could be referred to as management-induced niche shifts.

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