The effects of interspecific competition on African cheetah (*Acinonyx jubatus*) foraging success and diet breadth

Jamie Smith

November 19, 2012
BIOS 3010
Department of Biological Sciences,
Western Michigan University,
Kalamazoo, Michigan 49008, U.S.A.
Introduction

Interspecific competition is an ecological interaction that can have a powerful and widespread impact on community composition as species influence each others' distribution and abundance, potentially determining whether species will be able to coexist (Henke and Bryant 1999, Begon et al. 2006). Predators also have various levels of impact on prey populations through top-down effects (Sinclair et al. 2003), although Bertram (1979) found predation to have a weak effect, if any, on prey populations. Broadly, interspecific competition results in one of two occurrences: coexistence or competitive exclusion (Begon et al. 2006), both of which have implications for conservation efforts involving endangered species (Laurenson 1995, Linnell and Strand 2000). Several large African carnivores are vulnerable or endangered (IUCN Red List of Threatened Species), and competition for resources is often a contributing factor to such population reductions (Begon et al. 2006). The asymmetry of competitive ability among organisms will favor some species while others will suffer reduced fitness, even if they are able to sustain their populations at reduced levels (Begon et al. 2006). The intensity of interspecific competition increases with increasing trophic level as food and energy sources become more limited and thus can be particularly strong and extensive within large predator guilds (Caro and Stoner 2003).

Interspecific competition has been observed among African predators (Creel and Creel 1996, Linnell and Strand 2000, Caro and Stoner 2003). Carbone et al. (1999) estimate that carnivores greater than 20 kg in size typically consume prey that is over 45% of their own body weight, and many of them hunt similarly sized prey (Owen-Smith and Mills 2007). Prey size also influences feeding frequency; the greater amount consumed, the longer a predator will wait between feedings. Lions, opting for larger prey, tend to feed about every three days, while cheetahs, due to their smaller size and hunting style, feed on relatively smaller prey, but feed more frequently to maintain energy (Schaller 1972). The need to feed regularly and to a degree that maximizes energy benefits from the costs of stalk-and-chase hunting, which is common to several large African carnivores, results in a guild of large predators that form around a particular prey selection (Houston 1979).

The large African predator guild is composed of five carnivore species: the lion (Panthera leo), leopard (Panthera pardus), cheetah (Acinonyx jubatus), wild dog (Lycaon pictus) and spotted hyena (Crocuta crocuta) (Bertram 1979, Owen-Smith and Mills 2008). They interact as competitors for food and space, sharing a similar niche, while still maintaining some separation through prey specialization (Bertram 1979), and some also act as predators toward other members of the guild (Caro and Stoner 2003). Caro and Stoner (2003) found that geographic range overlap between cheetahs and 24 other African predators exceeded 33 percent, which increases the likelihood of carnivore interactions and potential competition. Cheetahs cover extensive ground when searching for prey (Caro 1994), and the majority of their prey is migratory (Bertram 1979), increasing their range and the likelihood of overlap with other members of the predator guild. As stalk-and-chase hunters that pursue prey at very high speeds, they tend to hunt more successfully in large, open spaces (Mills et al. 2004). Prey densities also factor into estimates of space requirements; even in predator-free environments, if the prey density is low, cheetahs will require more geographical space to support the population (Lindsey et al. 2011).

Cheetahs tend to hunt medium-sized prey (18-65 kg) (Bloomhall 2001, Hayward et al. 2006). Lions prefer larger prey than cheetahs, but they frequently take medium-sized prey, demonstrating a tendency toward opportunistic hunting (Hayward and Kerley 2005), which creates a dietary overlap between lions and cheetahs despite their differing ideal prey sizes (Figure 1).
Figure 1. Proportion of kills made by each guild member per body mass of prey. Lions, hyenas, leopards, and wild dogs all have the potential for dietary overlap with cheetahs (Owen-Smith and Mills 2007).

Cheetahs are unable to behave as contest competitors because their populations exist at low densities (Bertram 1979). They tend to be scramble competitors, rather than interference, probably due to their smaller size relative to other key members of the guild and their solitary hunting style. Their inability to defend against attacks by lions or hyena packs makes them subordinate within the guild (Hayward and Slotow 2009) and also exposes them to a greater risk of contest competition, predominantly through kleptoparasitism (Caro and Stoner 2003). Cheetahs are among the carnivores most vulnerable to kleptoparasitism, with as many as 10 species able to act as kleptoparasites (Caro and Stoner 2003). Lions and hyenas are the most common kleptoparasites of cheetah kills, responsible for 78% and 15% of kleptoparasitism events respectively in one community (Hunter et al. 2007b) (Figure 2).
In addition to competitive pressures, cheetahs are also predated by other members of the guild. Lions and hyenas are responsible for the majority of cub deaths. Laurenson (1995) found that approximately 73 percent of cub kills in a Serengeti cheetah population were caused by lions and 15 percent by hyenas. Predation of adult cheetahs is less frequent, although it occurs occasionally. This predatory interaction between cheetahs and their main competitors makes it difficult to distinguish between the relative impacts of predation and competition on avoidance behavior.

Interspecific competition has ecological significance because it affects abundance and distribution of species (Begon et al. 2006). Competition between large carnivores impacts the structure of multiple trophic levels and biodiversity (Terborgh 1992, Woodroffe and Ginsberg 2005, Terborgh and Estes 2010). My goal is to understand the effects of interspecific competition on cheetah foraging and diet breadth, so here I review the literature to test the null hypothesis that interspecific competition has no effect on cheetah diet breadth and foraging success. My alternate hypothesis is that interspecific competition will cause cheetahs to have reduced foraging success and limit their diet breadth.

Materials and Methods
I utilized multiple journal databases made available through Western Michigan University’s library website, primarily Web of Science and ScienceDirect. Approximately thirteen hours were spent searching databases and browsing the results for relevant articles. I searched both databases using various combinations of the following search terms: cheetah, hunt*, forag*, compet*, interspecific, diet, carnivore. ScienceDirect produced greater numbers of articles per search than Web of Science (Figure 3), but the percentage of relevant articles retrieved from the search results was much greater with Web of Science (Figure 4).
Figure 3. Number of hits produced per search terms per database. ScienceDirect produced greater numbers of articles per search than Web of Science.

Figure 4. Percentage of relevant articles found per search terms per database. Web of Science produced a greater percentage of useful articles per search than ScienceDirect.
Results

Direct Effects of Interspecific Competition

i. Space and resource limitations

Space is among the most limiting resources for African wildlife communities, and the less space that is available to large carnivores, the more they will be forced to interact. Lindsey et al. (2011) estimated that a group of ten to fifteen cheetahs requires as much as 466 km\(^2\) in predator-free areas, and up to 3,739 km\(^2\) when sharing space with competitors. In spite of their clear need for extensive space, cheetahs have not yet been outcompeted by stronger competitors. Durant (1998) suggested that cheetahs are able to coexist with superior competitors because of their mobility and capacity to successfully avoid interacting with competitors without expending excess energy. Their tendency to forage over broad ranges and follow migratory herds of prey may help them to avoid aggregations of competitors.

ii. Habitat variation

Cheetahs typically hunt in grasslands, and most studies take place in these open prairies (Schaller 1972, Durant et al. 1988, Fitzgibbon 1990, Laurenson 1995, Durant 1998). However, a study by Broomhall (2001) has shown that cheetahs can inhabit thickets and wooded areas, possibly to a) exploit higher prey densities, b) conceal themselves from prey for stalking, and c) conceal themselves from competitors. They preferred habitats with both open grasslands and brush/woodland cover, rather than one habitat type exclusively. Such habitat preference is likely due to the fact that they hunt significantly more often and make more kills in the savanna, but enjoy reduced kleptoparasitism risk and frequency in the brush. Greater proportion of cover was associated with shorter chase distance, greater hunting success, and less kleptoparasitism (Figure 5).

Bissett and Bernard (2006) found similar results, observing that more hunts occurred in the open than in the thicket, but successful kills were made by both males and females within the brush. A coalition of three males made two kills out of three attempts in the brush, as opposed to five kills out of eleven attempts in the open. Females with cubs had three kills out of five hunts in the thicket, and two kills out of five hunts in the open, while single females had two unsuccessful hunts in the thicket and three kills out of four hunts in the open. These results demonstrate that cheetahs, while preferring to hunt in the open, can still make successful kills in brush. Such a habitat would not be conducive to high speed chases, but may offer a good trade-off, particularly for females with cubs, by providing concealment from prey for ease of stalking, from competitors to reduce the risk of kleptoparasitism, and from predators that might kill the cubs.
Figure 5. Correlation between amount of cover and a) chase distance, b) hunting success, and c) kleptoparasitism per location (Broomhall 2001).
iii. Avoidance behavior

Laurenson (1995) observed that vigilance at kills was significantly higher among lactating females and females with cubs than other cheetahs, and concluded that this was due to the risk of cub predation by other competitors. This behavior was also observed by Hunter et al. (2007b), suggesting that avoidance behaviors may also be a response to predation risk. Durant (2000) observed cheetah behavior in response to lion and hyena playbacks and found that vigilance, movement patterns, and cheetahs were significantly less likely to hunt after hearing lion playbacks (Figure 6). However, no significant difference in response depending on sex or reproductive status was observed, implying that avoidance behavior was a response to competition, rather than risk of predation. Bisset and Bernard's (2007) study took place in a community with a lion pride, and they observed that only the coalition would hunt near the lions; every other social group remained at least twice as far away, presumably to avoid competitive interactions, as females with cubs were kleptoparasitized three times by lions.

![Figure 6. Distance (m) of movement and probability of hunting after dummy playbacks with no sound (black), hyena playbacks (gray) and lion playbacks (white) (Durant 2000).](image)

**Indirect effects of interspecific competition**

i. Foraging decisions and hunting success

Cheetahs in the playback experiment that opted to hunt after hearing lion playbacks were less likely to make kills (Durant 2000). Cooper et al. (2007) found that foraging decisions were affected by the presence of lions. They did not, however, detect any significant effect on foraging decisions caused by hyenas. As observed in other studies (Durant 2000), cheetah behavior implies that they find lions to be more intense competitors than hyenas.
It is suggested that cheetahs select for low and intermediate density prey populations because they may seek to avoid competitive interactions with lions and hyenas, both of which aggregate around high density prey populations (Cooper et al. 2007). However, it is possible that cheetahs prefer smaller density herds because there is a hunting advantage (Fitzgibbon 1990).

ii. Diet breadth and prey selection may reduce susceptibility to competition

Cheetahs have fairly high degrees of dietary overlap with their competitors (Hayward and Kerley 2008) (Figure 1), but they select strongly for medium-sized prey (Hayward et al. 2006), particularly Thomson's gazelles (Fitzgibbon 1990), and also include Grant's gazelles, impala, blesbok, and springbok, among others in their diet (Hayward et al. 2006). One specific advantage of hunting relatively smaller prey is the decrease in retention time after the kill. Medium-sized prey can be consumed at greater speed, reducing the amount of time spent at the kill, and thus the risk of kleptoparasitism. Medium-sized prey are also easier for cheetahs to subdue, given that they are solitary hunters and relatively small predators (Hayward et al. 2006).

iii. Temporal separation between cheetahs and competitors

Cheetahs are most active at dusk, while their most intense competitors, lions and hyenas, are predominantly nocturnal, creating less than 55 percent activity overlap in time with the other main guild predators (Hayward and Slotow 2009) (Figure 7). This is a fairly small overlap relative to the 89 percent overlap suffered by lions and 81 percent by leopards, and supports Hayward and Slotow’s (2009) hypothesis that carnivores subject to intraguild predation would alternate their activity times with their main competitors to avoid such interactions. In spite of the dietary overlap between hyenas, lions, and cheetahs, temporal separation of foraging reduces their competitive interactions (Hanby and Bygott 1979). Figure 7. Temporal activity overlap among large African predator guild members (Hayward and Slotow 2009).

![Figure 7](image-url)
Discussion and Conclusion

Based on evidence from my literature review, I reject my null hypothesis that interspecific competition has no effect on cheetah foraging success and diet breadth, and accept my alternate hypothesis. Cheetah foraging and diet is influenced by a number of factors, and the interactions are far more complex than a single cause-and-effect relationship, but there is evidence supporting the idea that interspecific competition influences foraging success and diet. Kleptoparasitism directly impacts hunting success, and the risk of kleptoparasitism can cause avoidance behaviors that impact foraging success and potentially increase energy costs by causing cheetahs to choose not to hunt, or to hunt less successfully (Durant 2000).

However, there are a number of ways in which these negative impacts are balanced, allowing cheetahs to coexist in the community. The flexibility of hunting in wooded habitats shows potential to increase their overall hunting success by reducing the risk of kleptoparasitism and providing an environment that increases their stealth (Broomhall 2001, Bissett and Bernard 2007). Opting to hunt from low-density prey populations reduces the frequency of their interactions with their main competitors (Cooper et al. 2007), and temporal separation allows cheetahs to avoid competitive interactions with their nocturnal competitors (Hayward and Slotow 2009).
Literature Cited


