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Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures

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ABSTRACT

Although carnivores are in global decline, diverse carnivore communities are common in sub-Saharan Africa, where more than 20 species may co-occur. Though intraguild competition and predation can limit the set of species that coexist, most carnivores have traits that decrease the impacts of interspecific competition on fitness, a pattern that promotes coexistence. An increasing human population and demand for natural resources (e.g. farming) has fragmented landscapes, reduced available prey, and elevated rates of conflict. These anthropogenic pressures tend to eliminate large carnivores first, which can have cascading effects on ecosystem function (e.g. mesopredator release). Anthropogenic pressures might also affect mesocarnivores directly, but this hypothesis has received little research attention to date. Here, we used camera surveys to describe spatial and temporal patterns of carnivore occupancy in a mixed-use landscape in Kenya. This landscape included a community conservation area and seasonally occupied human settlement and livestock grazing areas. We detected 21 carnivore species and examined occupancy patterns for the 12 most frequently detected. Differences among species in responses to environmental conditions supported a hypothesis of spatial niche partitioning. Differences in the temporal activity patterns of the apex predators and mesocarnivores supported a hypothesis of temporal niche partitioning. Human land use altered occupancy patterns in 10 of 12 species. Apex predator occupancies were lower in more anthropogenically disturbed areas, but mesocarnivore occupancies were not inversely related to apex predators, contrary to the mesopredator release hypothesis. Our results suggest that a diverse carnivore community persists in this mixed use landscape because of seasonal variation in human land use.

1. Introduction

There has been substantial research on the influence of bottom-up processes on carnivore populations (Creel et al., 2001), and this work clearly establishes the importance of habitat loss and prey depletion for carnivore conservation. However, the top-down process of intraguild competition and predation also influences carnivores' abilities to carve out ecological niches, which can affect distributions and abundances (Caro and Stoner, 2003; Creel et al., 2001; Palomares and Caro, 1999; Ritchie and Johnson, 2009). Several aspects of carnivore ecology probably strengthen the effects of interspecific competition in this guild. Most obviously, carnivores are morphologically and behaviorally adapted to killing, which can increase the likelihood that interference competition leads to intraguild predation (even though the killed competitor is frequently not consumed) or displacement from preferred habitats. Additionally, the energetic costs of active hunting are high in comparison to most other foraging strategies (Creel and Creel, 1995; Gorman et al., 1998), and this strengthens selection in favor of kleptoparasitism from sympatric species even when live prey are abundant. For example, competitively dominant spotted hyenas (*Crocuta crocuta*) sometimes follow hunting groups of African wild dogs (*Lycaon pictus*), a subordinate competitor, to outnumber and steal their kills. (Creel and Creel, 1996; Estes and Goddard, 1967; Fanshawe and Fitzgibbon, 1993; Malcolm and Marten, 1982). Thus, interactions within a carnivore community can decrease a species' fitness (Creel and Creel, 1996; Gorman et al., 1998; Linnell and Strand, 2000) and increase the probability of a species' local or global extinction (Polis et al., 1989).

To offset the costs of interspecific competition, natural selection favors adaptations of morphology, life history, and behavior that limit the negative effects of competition on fitness (Creel et al., 2001; Hardin, 1960; Pfennig and Pfennig, 2005), and thus promote coexistence. Such niche partitioning is apparent in most carnivore guilds, where numerous physical traits (e.g. body size, stature, dentition, specialized sensory systems) and behavioral/ecological

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traits (e.g. solitary vs social, habitat and dietary preferences) have allowed competing species to coexist by partitioning resources (Fedriani et al., 2000; Karanth and Sunquist, 1995; Kitchen et al., 1999; Mills et al., 1984; Owen-Smith and Mills, 2008; Sinclair et al., 2003). Though the causal mechanism driving the evolution of physical attributes and behavioral strategies is often uncertain (e.g. sociality, (Nudds, 1978; Waser, 1981)), differences among species in derived characteristics promote coexistence, and many of the differences within carnivore communities are probably directly linked to competition. For example, attributes of skull morphology and dentition are uniformly distributed within guilds, as expected under the hypothesis that competition drives niche partitioning (Dayan et al., 1992). Active spatial and temporal avoidance at broad (geographic) scales and fine (habitat) scales can reduce the frequency of potentially costly encounters between a subordinate and dominant competitor (Creel et al., 2001; Durant, 1998; Fedriani et al., 2000; Hayward and Slotow, 2009; Linnell and Strand, 2000; Mills and Biggs, 1993; Neale and Sacks, 2001). These avoidance behaviors have been well-documented in the African wild dog and cheetah (*Acinonyx jubatus*), which avoid areas of high prey density because the competitively superior lion (*Panthera leo*) and spotted hyena prefer these areas (Durant, 1998; Creel and Creel, 2002).

Carnivores evolved their adaptations to interactions with guild members within large, heterogeneous ecosystems (Creel et al., 2001). However, an increasing human population and concomitant demand for land and natural resource extraction have fragmented landscapes, reduced available forage and prey items for carnivores, and increased the interface between people and carnivores (Woodroffe and Ginsberg, 1998; Woodroffe, 2000). Patterns of human land use change coupled with a decreased tolerance of conflict-prone species pose a threat to carnivore community structure and dynamics. In particular, large and competitively dominant species that pose a threat to human livelihoods have experienced drastic population reductions and shrinking distributions (Ray et al., 2005; Woodroffe and Ginsberg, 1998; Woodroffe, 2000). For instance, the African lion population in Kenya has declined from approximately 2750 individuals to 2000 in 10 years, a decline of nearly 30% (Kenya's National Large Carnivore Task Force, 2008). Data on direct anthropogenic pressures on many smaller, co-occurring carnivores are sparse and the impacts are not as well understood (Martinoli et al., 2006; Pettorelli et al., 2010; Schipper et al., 2008). Nevertheless, fragmentation of carnivore communities and reductions in species richness have been described in disturbed areas (Dalerum et al., 2009). In most of the world, radical changes in the relative frequency of carnivore species have likely altered community function. For example, declines of a dominant species may prove advantageous to a subordinate species via numerical 'release' (i.e. mesopredator release), triggering cascading ecological effects (Crooks and Soulé, 1999; Ritchie and Johnson, 2009).

Alternatively, variation in human land use may help sustain native species richness in some taxa. For example, Gardner et al. (2007) showed that species richness in small mammals, amphibians, birds, butterflies, and trees did not change, but the composition of species did change across a gradient of land uses from strictly protected parks to areas of high human activity. Thus, heterogeneity in local land uses may protect or promote biological diversity at the regional scale, by creating areas with complimentary sets of species. This hypothesis is largely untested for carnivore communities. For example, in Serengeti National Park, lion and spotted hyena densities have increased in recent decades, resulting in reductions in the African wild dog and cheetah populations inside the park (Hanby and Bygott, 1995). Outside the park, however, densities of lions and spotted hyenas have been reduced by trophy hunting (Packer et al., 2011) and human persecution, respectively, allowing African wild dogs and cheetahs to persist (Creel et al., 2001). In addition to numerical changes, human land use may also induce behavioral adjustments. For example, heavily persecuted species, such as the spotted hyena, can become more secretive or nocturnal in heavily human-modified landscapes (Boydston et al., 2003). Such behavioral changes in a dominant species may initiate a 'behavioral release' in subordinate competitors via broadening of temporal niches. Thus, while habitat loss, prey depletion, and overharvest make strictly protected areas of great importance for large carnivores (Cooley et al., 2009; Creel and Rotella, 2010; Packer et al., 2009; Robinson et al., 2008), these results suggest that richer and more diverse carnivore communities might be maintained in landscapes incorporating a mix of protected and human land uses, particularly when a community includes subordinate species excluded from fully protected areas by dominant species (Creel et al., 2001; Noss et al., 1996). Independent of this hypothesis, conservation and management requires an understanding of the dynamics of carnivore communities outside of fully-protected national parks, and such dynamics have been little-studied in Africa.

We used camera trapping and dynamic occupancy modeling (Fiske and Chandler, 2011; MacKenzie, 2003; MacKenzie et al., 2006) to examine the distribution of a diverse carnivore guild across a multiple human use landscape in Kenya's southern Rift Valley. This landscape is occupied by pastoralist Maasai people, and includes a community-run conservation area (CCA), seasonal livestock grazing grounds, and areas of permanent human settlement and use. This study was motivated by a lack of quantitative data on African carnivore communities across a range of human land uses. In addition, though the predominant form of land use in the southern Rift Valley is the rearing of livestock across an unfenced rangeland, many other East African rangelands are being subdivided and converted to farmland (Homewood et al., 2009). This regional trend could present a challenge to land use policy, wildlife management, and conservation strategies in the southern Rift Valley.

Our primary objectives were to quantify species richness, evaluate the impacts of environmental features and anthropogenic pressures on species occupancy patterns, and test for spatial and temporal niche partitioning among species across this multiple human land use landscape. Specifically, we tested the following hypotheses: (1) the combination of environmental conditions affecting occupancies will be unique for each species, creating a pattern of spatial niche partitioning within the local carnivore community, (2) small and medium-sized species occupancies will be higher in areas where large carnivore occupancies are low due to mesopredator release, (3) where large carnivore occupancies are high, temporal activity patterns of small and medium-sized species will be driven by temporal avoidance of lions and spotted hyenas, creating a pattern of temporal niche partitioning (Mills and Biggs, 1993), and (4) occupancies of conflict-prone species that directly threaten livestock (lions, spotted hyenas) will be more directly influenced by anthropogenic pressures than smaller, non-conflict species.

2. Materials and methods

2.1. Study area

This study was conducted in the southern Rift Valley of Kenya on the Olkiramatian and Shompole Maasai Group Ranches (GRs) (~1000 km^2). The full study area supports a low-density human population of Maasai pastoralists (~10 people/km^2) and their livestock, which occur at moderate to high densities (sheep/goats: 59.1 ± 17.0 individuals/km^2, cattle: 15.8 ± 5.7 individuals/km^2) (Schuette, 2012). Despite increasing land subdivision and farming on surrounding rangelands (Homewood et al., 2009), the Olkiramatian and Shompole Maasai community continue to practice a semi-nomadic lifestyle, which is based on seasonal movements with their livestock to access grazing areas. This land use system