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Diel patterns of movement activity and habitat use by leopards (*Panthera pardus pardus*) living in a human-dominated landscape in central Kenya

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ABSTRACT

Large carnivores can exert strong influence on local ecosystems, making them important targets for biodiversity conservation. An important question for conserving large carnivores outside of protected areas is the role of human activity in influencing the behavior of these predators. We used high-resolution animal location tracking and statistical modeling to examine the behavior of seven leopards (*Panthera pardus*) occupying an area that includes a research center and livestock ranch in central Kenya. Our analyses reveal changes in habitat selection around the times of sunrise and sunset, corresponding with changes in human activity at our site. Activity patterns were also variable within and among the leopards in our sample. To explore sources of this variability, we used regression modeling to estimate the relative influence of changing spatial and environmental conditions for leopard ranging behavior. Despite the tendency to be active during the day, we found that leopards strongly avoided areas where they were likely to encounter people during the daytime and showed variable selection for these same areas at night. The use of anthropogenic habitats was also associated with periods of greater ranging activity. We discuss the implications of these results for conservation efforts that attempt to balance the demands of livestock ranching alongside carnivore conservation.

1. Introduction

Large mammalian carnivores are ecologically important because they can regulate primary consumers, thereby having an indirect positive effect on plant biomass and maintaining ecosystem functions (Ford et al., 2014; Ripple et al., 2014). But many populations of large carnivores occur outside of protected areas where they are threatened by declining availability of wild prey, habitat loss, and lethal retaliation from humans over attacks on domesticated animals (Woodroffe et al., 2005; Ripple et al., 2014). As a result, developing strategies to promote the coexistence of people and predators outside of protected areas has been an important goal in carnivore conservation (Treves and Karanth, 2003; Lute et al., 2018).

In East Africa, addressing this issue is especially critical because the region contains some of the greatest diversity of large carnivores in the world. However, many of these species are also threatened, as a result of habitat loss and other conflicts with humans associated with agricultural and urban developments (Ogutu et al., 2011; Ripple et al., 2014). Livestock production is one of the primary land uses in the region's arid and semi-arid savanna grasslands, and with global demand for livestock production projected to increase into the future, understanding the impact of these changing land use systems for the behavior and ecology of large carnivores is therefore an important question for conservation planning in these increasingly human-dominated landscapes (Ripple et al., 2014).

Advancements in animal tracking technology have now made it possible to gain unprecedented behavioral insights from cryptic carnivore species, leading to renewed interest into the ecological consequences of anthropogenic disturbances that alter predator behavior (Kuijper et al., 2016; Smith et al., 2015). Because carnivores can have disproportionate influence in trophic webs, the effects of human activity and landscape change on carnivore behavior can have cascading consequences for the local ecosystem, even if disturbances are non-lethal (Hebblewhite et al., 2005; Oriol-Cotterill et al., 2015b; Kuijper

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et al., 2016). Many animals react to non-lethal anthropogenic disturbances by altering their habitat preferences, engaging in evasive movements, increasing their levels of vigilance at the expense of foraging, and decreasing the amount of time spent in productive habitats (Frid and Dill, 2002). Moreover, in many cases anthropogenic influence extends far beyond wild animals' immediate surroundings. Pedestrian and vehicle traffic may cause animals to flee or increase their levels of vigilance even at distances over 0.5 km away (Andersen et al., 1996; Andersen and Aars, 2007). Extensive networks of roads, trails, or other landscape features associated with human movement can also alter how animals assess and use their habitats (Benitez-López et al., 2010), and impact the structure of the local animal community in ways similar to lethal activities (Griffiths and van Schaik, 1993).

Behavioral insights from animal tracking data could help to clarify the impact of livestock ranching and other forms of human activity for carnivores in East Africa. In Laikipia, Kenya, protected areas for the region's diverse and abundant wildlife are almost entirely privately owned, and, in many cases, attempt to remain profitable through a combination of livestock ranching and wildlife tourism (Georgiadis, 2011). This land use strategy creates incentives for property owners and local communities to treat wildlife as valuable resources and adopt policies favorable to their conservation, such as not constructing fences that impede their movements, stocking sustainable densities of livestock to avoid overgrazing, and banning the use of lethal control against carnivores (Georgiadis, 2011).

The livestock husbandry practices used by the region's pastoralists can also modify the environment in ways beneficial for wild and domestic animals. Glades are the sites of abandoned pastoralist settlements where livestock were corralled overnight in fenced structures called *bomas*. Wild herbivores and livestock use these treeless sites because the short, rich grasses provide high quality foods that serve as important resources in nutrient-poor savannas (Augustine et al., 2011) and the greater visibility within glades offers protection from predators (Ford et al., 2014; Riginos, 2015). The intensive use of glades by wild herbivores maintains these key resources for decades or more, where they function as important drivers of the seasonal and spatial distribution of mammalian herbivores (Veblen, 2012). As a result, mixed-use conservancies in Laikipia support a rich abundance and diversity of wild animals, including populations of large carnivores, comparable to those found in areas designated only for tourism (Kinnaird and O'Brien, 2012).

Conservancies and similar land use systems that try to promote livestock ranching alongside wildlife conservation therefore appear promising for preserving biodiversity outside of formal protected areas. Implementing these land use strategies is particularly important in Kenya where an estimated 65% of wildlife occurs outside of protected areas (Western et al., 2009; Ogutu et al., 2011). An important unanswered question for mixed-use conservancies, however, is how the persistent disturbances associated with ranching operations shape the activity patterns and spatial ecology of large carnivores.

We sought to answer this question by studying the movement behavior and activity of seven leopards (*Panthera pardus pardus*) occupying a conservancy and livestock ranch in central Kenya. We use high-resolution animal tracking and fine-scale environmental data to examine how temporal and spatial patterns of habitat use and activity might be shaped by anthropogenic disturbance cues by documenting patterns of leopard movement behavior and habitat selection over the diel period. We find that leopards tended to avoid anthropogenic habitats at all hours of the day, but that patterns of avoidance were strongest during the daytime. We next used exploratory statistical modeling to examine how activity allocation between the day and night was influenced by variation in habitat use and temporally varying environmental factors. Differences in habitat use were generally poor predictors of leopard ranging activity, except for the use of anthropogenic habitats, which were associated with periods of greater movement activity. However, our modeling found that variation in leopard movement activity was not well explained by diel period. Instead, variation in activity allocation across the day and night was more strongly influenced by the lunar phase.

2. Materials and methods

2.1. Data collection

The data presented here were collected at the Mpala Research Centre (MRC), a 211 km^2 privately-owned wildlife conservancy and livestock ranch located in Laikipia region of central Kenya (0.29 N, 36.90 E; Fig. 1). MRC is located in a high elevation (1800 m a.s.l.) semi-arid savanna ecosystem dominated by thorny *Vachellia* (*Acacia*) species (especially *V. brevispica* and *V. etbaica*) and grasses from the genera *Cynodon*, *Pennisetum*, *Digitaria*, and *Sporobolus*. Riparian areas along the Ewaso Nyiro River are characterized by fever trees (*V. xanthophloea*) and are an important water source for wildlife and livestock. The site receives approximately 600 mm of rain per year with monthly precipitation following a weakly trimodal seasonal pattern (Young et al., 1995). The site contains a largely intact mammal community.

The activities and living accommodations of livestock ranchers, staff, and researchers are heavily intermixed, and involve movements on foot and by motor vehicle through the landscape. As a result, contrasting predictions for different types of activities could not be made. However, the combined presence of researchers, students, ranch employees, and livestock make MRC comparable to conditions leopards and other animals experience on conservancies in Laikipia. MRC hosts Kenyan and international scientific researchers as well as undergraduate student groups. Livestock graze vegetation throughout the property and the livestock husbandry practices used at MRC closely resemble those traditionally used by the Laikipiak and Maasai pastoralists that inhabited the region prior to European colonization (Young et al., 1995) and which are still practiced on community rangelands (Woodroffe et al., 2005). These include following livestock on foot during the daytime and corralling them in bomas at night to deter thefts and attacks by carnivores.

A field team captured four female and three male leopards using foot-snare trapping methods as described in Frank et al. (2003). Leopards were trapped, and in three instances re-trapped, over two field seasons spanning a total of 14 months. During the first season, leopards were fitted with collars that recorded GPS locations at synchronous 15-min intervals each day starting at midnight. During the second season, we deployed SMART collars (Williams et al., 2014) that sampled locations every 5 min. To make inferences across the diel period, we subsampled the locations collected during the second season to the same 15-min time intervals as the data collected during the first season. Information on the dates and duration of individual leopard movement paths can be found in Appendix A.

We used a base station (e-obs GmbH, Gruenwald, Germany) and a nine-element Yagi antenna (YAGI-869A: Low Power Radio Solutions, Witney, United Kingdom) or an omni-directional marine antenna (cxl 900-3LW: Procom, Frederikssund, Denmark), to download GPS data remotely when within UHF range of each collar throughout the first season. During the second season, GPS data were downloaded each day using Iridium satellite uplink or a handheld UHF base station. Each leopard was tracked for an average of 3.8 months (range: 1.7–7.8 months) before equipment failure or because the collar's lifespan ended.

2.2. Temporal movement activity, space use, and habitat selection

To characterize movement behavior from GPS tracks, we calculated the linear displacement and change in heading between successive leopard relocations during each 15-min time window. A multilevel bootstrap procedure was then used to estimate the average distance moved and movement directionality by leopards during each time