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Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot

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ABSTRACT

Leopard population declines largely occur in areas where leopards and people frequently interact. Research on how leopards respond to human presence and competitors, like other predators, can provide important insights on leopard ecology and conservation in human-dominated regions; however, such research is lacking. Here we used data from field cameras in 2010 and 2011 to examine how human presence, prey, and tigers influence leopard spatiotemporal activity patterns in and around Nepal's Chitwan National Park, part of a global biodiversity hotspot. We found that leopards were adjusting their spatiotemporal activity patterns to both tigers and people, but by different mechanisms. Leopards spatially avoided tigers in 2010, but were generally active at the same times of day that tigers were. Despite pervasive human presence, people on foot and vehicles had no significant effect on leopard detection and space use, but leopard temporal activity was displaced from those periods of time with highest human activity. Temporal displacement from humans was especially pronounced outside the park, where there is a much greater prevalence of natural resource collection by local people. Continuing to evaluate the interconnections among leopards, tigers, prey, and people across different land management regimes is needed to develop robust landscape-scale conservation strategies.
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1. Introduction

Leopards (*Panthera pardus*) are a top predator found throughout Africa, the Middle East, and Asia (Henschel et al., 2008). On one hand, they provide a number of key ecosystem functions, including the regulation of ungulate populations and suppression of mesopredators (Ripple et al., 2014). For example, trophic cascades in West Africa have occurred after declines in top predators, including the leopard, with unpredictable and often negative consequences on human communities (Ripple et al., 2014). On the other hand, although leopards are relatively widespread, the International Union for the Conservation of Nature indicates that leopards may soon qualify as "vulnerable" to extinction due to rapid declines in their numbers throughout much of their range (Henschel et al., 2008). Declines in leopard populations are largely the result of hunting for trade and human-induced habitat loss and fragmentation (Henschel et al., 2008). People also indiscriminately kill leopards in defense of humans and livestock (Ray et al., 2005).

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Given the frequency of interactions with people, it is important to ascertain how leopards respond to people and the mechanisms that govern those responses. However, there are few studies evaluating how humans impact fine-scale spatial (∼1 km) and temporal activities (diel time scale) of leopards (Kawanishi and Sunquist, 2004; Ngoprasert et al., 2007; Henschel et al., 2011). The nature of the relationships between people and leopards indicated by these studies, however, are equivocal. In central Gabon, for example, Henschel et al. (2011) found that leopard density decreased closer to human settlements. In Kaeng Krachan National Park, Thailand, Ngoprasert et al. (2007) found that leopards avoided human traffic inside the park in both space and time. In contrast, Kawanishi and Sunquist (2004) found no significant effect of human traffic on leopard spatiotemporal activity in Taman Negara National Park, Peninsular Malaysia.

Humans are not the only factor potentially affecting leopard behaviors and activities. Interspecific competition with other sympatric large carnivores may also impact leopard spatiotemporal activities (Seidensticker, 1976; Karanth and Sunquist, 2000; Hayward and Slotow, 2009; Wang and Macdonald, 2009; Odden et al., 2010; Vanak et al., 2013). For example, the tiger (*Panthera tigris*) is a key competitor across much of the leopard's range in Asia. Tigers are considered socially dominant to leopards (Seidensticker, 1976; Karanth and Sunquist, 2000; Odden et al., 2010). However, the impacts of tigers on leopard spatiotemporal activities differ across sites, with some studies indicating leopards avoid tigers in space and time (Seidensticker, 1976; Odden et al., 2010; Steinmetz et al., 2013), whereas other studies indicate high levels of spatiotemporal overlap (Karanth and Sunquist, 2000; Azlan and Sharma, 2006; Ramesh et al., 2012). Nevertheless, prey clearly plays a key role in mediating tiger–leopard interactions (Seidensticker, 1976; Karanth and Sunquist, 2000; Wang and Macdonald, 2009; Odden et al., 2010). Many regions support commingling populations of leopards, their competitors, and people. Research that quantitatively evaluates the impacts of both people and competitors on leopard spatiotemporal activity can provide important insights on leopard ecology and conservation in human-dominated regions, which prevail throughout the leopard range. However, there is a paucity of such research.

To help fill these information gaps, we examined how human presence, tigers, and prey influence leopard spatial and temporal activity patterns in and around Nepal's Chitwan National Park, part of a global biodiversity hotspot (Myers et al., 2000). The park (932 km^2), established in 1973, supports both leopards and tigers as well as various prey species, including spotted deer (*Axis axis*), barking deer (*Muntiacus muntjak*), hog deer (*Axis porcinus*), gaur (*Bos gaurus*) wild boar (*Sus scrofa*), and sambar (*Rusa unicolor*) (Bhattarai and Kindlmann, 2012; Carter et al., 2012; Thapa et al., 2014). A buffer zone (750 km^2) surrounding the park was established in 1996. The buffer zone includes several forest tracts, but also includes human settlements with a growing human population estimated at over 300 000 in 2010 (UNEP/WCMC, 2011). Regular human presence in the forests inside the park and outside the park in the buffer zone consists mostly of people on foot, including local residents harvesting natural resources from the forest, tourists walking through the forest, and Nepal Army personnel who regularly patrol the park for illegal activities. In addition, vehicles carrying Army personnel and tourists are common on the forest roads.

We explore two hypotheses in this paper: (1) leopards adjust their spatiotemporal activity patterns to avoid people and tigers; and (2) leopard spatiotemporal patterns overlap those of major prey species. To test these hypotheses, we use recently-developed occupancy models that account for spatial autocorrelation, as well as spatially-explicit leopard density models and temporal activity and overlap analyses. The methodological tools and techniques used in this paper could be useful for assessing interspecific and anthropogenic impacts on various wildlife species in many regions around the world.

2. Materials and methods

2.1. Study site

Chitwan National Park (Fig. 1) (27°30′N–27°43′N, 84°9′E–84°29′E) is situated in south central Nepal. The park is located in a river valley basin along the flood plains of the Rapti, Reu, and Narayani Rivers with an elevation range of 150–815 m. Climate in Chitwan is subtropical with a summer monsoon season from mid-June to late-September, and a cool dry winter. The park and remaining forests in the buffer zone outside the park have retained the natural vegetation communities distinctive of the Himalayan lowlands, including *Sal* (*Shorea robusta*) forest, *khair* (*Acacia catechu*) and *sissoo* (*Dalbergia sissoo*) riverine forests, and grasslands dominated by species of the genera *Saccharum*, *Themeda*, and *Imperata* (Chaudhary, 1998; Carter et al., 2013).

2.2. Data collection and analyses

From January to May in 2010 and 2011 (i.e., the dry season before the monsoon), we used digital Reconyx RM45 passive infrared motion detecting cameras (Reconyx Inc., WI, USA) to determine the frequency of leopards, tigers, prey, and humans present at different locations within the study site. Motion-detecting cameras have been used in many other studies of leopards and tigers (Karanth and Nichols, 1998; Ngoprasert et al., 2007; Lynam et al., 2009; Carter et al., 2012; Athreya et al., 2013). In both years, we sampled the exact same locations inside and outside the Chitwan National Park in four successive blocks, each sampled for approximately 20 days at approximately 20 locations. The four adjoining sample blocks (with an aggregate area of approximately 100 km^2) encompassed naturally vegetated areas inside the park and in a forest tract in the buffer zone that surrounds the park. The sample blocks were oriented roughly parallel to the human settled area outside the park. Each block was initially subdivided into a grid with approximately twenty 100-ha cells. A camera pair (hereafter a 'camera trap') was located at or close to the center of each grid cell along the nearest forest road, path or animal trail with

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