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Spatiotemporal patterns of lion space use in a human-dominated landscape

A. Oriol-Cotterill [a, c, *], D. W. Macdonald [a], M. Valeix [a, b], S. Ekwanga [c], L. G. Frank [c]

[a] Wildlife Conservation Research Unit, Zoology Department, University of Oxford, Oxford, U.K.
[b] Laboratoire de Biométrie et Biologie Evolutive, Université Claude Bernard, Villeurbanne, France
[c] Living With Lions, Museum of Vertebrate Zoology, University of California, Berkeley, CA, U.S.A.

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The African lion, *Panthera leo*, is threatened throughout much of its remaining range by human impacts such as loss of prey, habitat fragmentation and direct human-caused mortality, often in response to livestock predation. Lions' ability to adjust their behaviour to reduce direct contact with humans may affect their survival. We used fine-scale GPS data to measure lions' response to humans at two scales: between land use types (commercial ranches versus pastoral lands) and with proximity to human-occupied locations (i.e. livestock enclosures: 'bomas') within commercial ranch land. Study lions on commercial ranches reacted to the location and activity levels of humans on the local scale, showing no overall spatial avoidance but fine-scale temporal partitioning in their use of areas in close proximity to bomas, being closest at times when human activity was lowest (i.e. between 2300 and 0500 hours). At the land use scale, however, lions showed significant (but not total) spatial avoidance of pastoral land, despite similar prey densities and habitat structure on both land use types, indicating that lions' ability to utilize pastoral land was limited by pastoral people. When lions did utilize pastoral land, they were more likely to do so during the dark hours, when people were confined to bomas, than during the daylight hours. Lions moved faster and straighter in pastoral lands and when close to bomas, indicating that they adjust 'how' they move in response to humans. They were found closer to bomas with increasing rainfall and decreasing moonlight. Overall, lion movements suggested an ability to partition their activities spatiotemporally with those of humans such that risk of human-caused mortality was minimized while use of a human-dominated landscape was maximized.

Persecution by humans as a result of livestock predation is a major cause of mortality among large carnivores and may threaten the viability of many populations (Macdonald & Willis, 2013; Woodroffe, 2000). Variations in human densities, distribution, land use, behaviours and attitudes towards conservation in general, and carnivores in particular, create spatial variation in the likelihood of human-caused mortality. The resultant complex peaks and troughs of spatiotemporal variation in human-caused mortality risk in which large carnivores exist is here referred to as the 'Landscape of Coexistence', and is similar to the 'Landscape of Fear' experienced by prey under threat of predation (Laundré, Hernández, & Altendorf, 2001). Large carnivores sharing the landscape with people may thus attempt to trade off activities that enhance their fitness, such as foraging near humans, against risk of human-caused mortality, ultimately resulting in a variety of heterogeneously distributed behavioural responses of large carnivores to the threat posed by people.

In this context, studies have predominantly focused on spatial avoidance of people by large carnivores (Boydston, Kapheim, Watts, Szykman, & Holekamp, 2003; Mattson, 1990; Schuette, Creel, & Christianson, 2013; Schuette, Wagner, Wagner, & Creel, 2013; Van Dyke et al., 1986). A carnivore's response to people, however, may not be as simple as straightforward avoidance of human-occupied areas (Kolowski & Holekamp, 2009). Such areas may contain valuable resources (e.g. livestock) or access to a limited resource (e.g. dry season water sources; Schuette, Creel, et al., 2013) such that complete avoidance would result in substantial foraging costs. Hence, large carnivores in Landscapes of Coexistence may use such human-occupied areas and behave adaptively by following strategies that optimize resource acquisition while minimizing contact with people, and hence the risk of human-caused mortality (Macdonald, Loveridge, & Rabinowitz, 2010).

* Correspondence: A. Oriol-Cotterill, Living With Lions, PO BOX 555, Nanyuki 10400, Kenya.
E-mail address: alayne.cotterill@gmail.com (A. Oriol-Cotterill).

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Behavioural responses to predation risk shown by herbivores and mesocarnivores suggest temporal partitioning of habitats and resources can be a strategy to reduce predation risk (Durant, 1998; Harrington et al., 2009; Kronfeld-Schor & Dayan, 2003; Linnell & Strand, 2000; Valeix et al., 2009). Large carnivores can become more nocturnal in human-occupied areas (e.g. all carnivores: Frank & Woodroffe, 2001; mountain lions, *Felis concolor*: Van Dyke et al., 1986; spotted hyaena, *Crocuta crocuta*: Boydston et al., 2003; Holekamp & Dloniak, 2010; African wild dog, *Lycaon pictus*: Rasmussen & Macdonald, 2012; tiger, *Panthera tigris*: Carter, Shrestha, Karki, Babu Pradhan, & Liu, 2012). Responding to human activity levels, rather than just their physical location through spatiotemporal avoidance, may 'fine-tune' a large carnivore's avoidance of people to allow use of human-occupied areas at times when risk of detection is lowest.

Additionally, the spatiotemporal partitioning of activities across Landscapes of Coexistence may allow carnivores to utilize areas in closer proximity to people in ways that reduce their risk of detection. Foraging, for example, may be associated with a higher risk of detection by people than moving quickly through an area (see Douglas-Hamilton, Krink, & Volrath, 2005; Graham, Douglas-Hamilton, Adams, & Lee, 2009; Wall, Wittemyer, Klinkenberg, LeMay, & Douglas-Hamilton, 2013 for examples in African elephant, *Loxodonta africana*). Carnivores may, therefore, be expected to take straighter, faster movement paths in human-occupied areas (Dickson, Jennes, & Beier, 2005; Elliot, Cushman, Macdonald, & Loveridge, 2014). The characteristics of an animal's movement path can reveal where, for how long and also 'how' an animal spends its time (Valeix et al., 2010). Movement parameters may thus allow measurement of changes in an animal's behaviour in response to people and livestock (e.g. Valeix, Hemson, Loveridge, Mills, & Macdonald, 2012). Finally, environmental variables that affect success at hunting wild prey, such as light levels and rainfall, which in turn affect visibility, vegetation cover, prey densities and vigour (Funston, Mills, & Biggs, 2001; Packer, Swanson, Ikanda, & Kushnir, 2011; Patterson, Kasiki, Selempo, & Kays, 2004; Van Orsdol, 1984) may affect the trade-off between the costs and benefits of killing livestock for large carnivores, thus limiting their spatiotemporal avoidance of people and livestock (see Theuerkauf, 2009).

The African lion, *Panthera leo*, is particularly vulnerable to direct persecution by people and is often the first large carnivore species to be eradicated when living alongside people and livestock (Woodroffe, 2001). Lions are, therefore, a revealing model for testing whether behaviour is adjusted as a result of human-caused mortality risk. We expect behavioural adjustment particularly among breeding female groups (prides; see Whitman, 2006), as they exhibit the strongest behavioural responses to predation risk in other species (e.g. Caro, 1987; Childress & Lung, 2003; Liley & Creel, 2007; Pangle & Holekamp, 2010a, 2010b). The spatiotemporal scales at which lions respond to the presence of people may determine the extent and cost of behavioural adjustments. In this study, we used movement data derived from GPS radiocollar data to compare the spatiotemporal behaviour of lions at two scales in the study area: a landscape scale response to land use and a local-scale response to actual locations of people and livestock. In particular, we predicted that lions should behave similarly to less dominant carnivores in response to predation threat by larger carnivores (Broekhuis, Cozzi, Valeix, McNutt, & Macdonald, 2013) and respond to human activity by avoiding areas with high risk of human-caused mortality at times when risk of detection by people is high but utilizing these areas during periods when risk of detection is low. Movement parameters were also analysed at the two scales to test the prediction that lions would move faster and straighter in areas where the risk of human-caused mortality is high. Finally, we predicted that lions' behavioural adjustments in response to people and livestock should be influenced by environmental conditions that affect their hunting success of wild prey and detection by people (Funston et al. 2001; Patterson et al. 2004; Schaller, 1972; Van Orsdol, 1984; Woodroffe & Frank, 2005). We thus explored the influence of rainfall and moonlight levels on spatiotemporal variations in the behaviour of lions in a human-dominated landscape.

METHODS

Study Site

This study was carried out in Laikipia County, Kenya. The area comprises a mosaic of different land use types and is a place where people, livestock, wild ungulates and all the local large carnivore species share the landscape (Georgiadis, Nasser Olweroa, Ojwang', & Romañach, 2007; Woodroffe & Frank, 2005). We selected a 2800 km^2 area in the north of the study area which included two land use types, livestock being the main source of income for both: (1) commercial ranches and (2) pastoral land. We selected pastoral areas where population densities of wild prey, and habitat structure, were similar to those on the privately owned commercial ranches with which we made comparisons, based on long-term aerial census data (Georgiadis et al., 2007). Both commercial ranchers and pastoralists used traditional livestock husbandry techniques: livestock was herded into bomas (i.e. livestock enclosures) at night for protection against thieves and large carnivores, and moved out to graze by day, guarded by herders (Frank, 2011; Ogada, Woodroffe, Oguge, & Frank, 2003; Woodroffe, Frank, Lindsey, ole Ranah, & Romañach, 2006). In recent years, boma construction on commercial ranches has advanced from the traditional thorn walls to include some stronger materials such as metal and stone. Additionally, only adult herders accompany livestock during the day on commercial ranches, whereas children are sometimes used to guard grazing livestock on pastoral land (Woodroffe et al. 2006). These differences in livestock husbandry standards, coupled with higher densities of livestock and people on the pastoral lands (Georgiadis et al., 2007), results in a higher potential for human–lion conflict over livestock predation where lions exist on pastoral land, although a lack of reporting in pastoral parts of the study area meant an actual comparison of human–lion conflict levels on the different land use types was not meaningful.

While there is no legal (trophy) hunting of lions in the study area, lions regularly attack livestock, and are killed by people in response, on both land use types (Frank, 2011; Ogada et al., 2003; Woodroffe & Frank, 2005). A 19.4% mortality rate for collared lions in the study area was recorded between 1998 and 2004, with 17 of 18 deaths of collared lions due to retaliatory killing by humans after predation on livestock (Woodroffe & Frank, 2005). During our study period (2009–2012), 17 collared lions were known to be killed by people, while two collared lions died of other causes. People, therefore, represent the main mortality risk to adult lions in the study area.

Data Collection

Lion movements

Five female lions from different prides using both land use types in the study area (Fig. 1) were equipped with a GPS Plus radiocollar (Vectronics Aerospace GmbH). Collared lions were all multiparous females that were members of a pride. We acknowledge that the sample size used in this study was small. Studies on pinnacle carnivores such as lions often suffer from small sample sizes as these species normally occur in low densities. This was further