



Original investigation

Habitat use responses of the African leopard in a human-disturbed region of rural Mozambique

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ABSTRACT

Leopard (*Panthera pardus*) populations across Africa are increasingly exposed to high levels of anthropogenic disturbance, and information on habitat use responses of leopards in human-disturbed landscapes can help inform status assessments and guide conservation interventions. Unfortunately, however, few studies have investigated leopard ecology in human-disturbed landscapes, particularly in Africa. We employed camera-trapping and occupancy modelling to provide inferences on leopard habitat use in a National Park in Mozambique impacted by subsistence farming and bushmeat poaching. Replicated detection/non-detection occupancy surveys were used to estimate site use by leopards in a representative area of the park, and to investigate relative impacts of environmental, conspecific and anthropogenic factors on leopard occurrence. The proportion of sites used by leopards was estimated at 0.814 (SE = 0.093), which is approximately twice the occupancy previously reported for lion (44%) and cheetah (40%) in the same area. Leopard presence was not strongly predicted by any of the covariates, indicating there were no strong limiting factors. While leopards generally avoided human settlements and were positively predicted by prey, results suggest that there was sufficient prey and space for the species to use most available habitats. The greatest contributing factor to leopard habitat use was a positive correlation with bushmeat poachers and lions. It is possible that these other predators provide a more accurate indicator of prey availability than our single-species indicator based on camera trap data. This study provides important novel information on habitat use by leopards in a system disturbed by rural human subsistence activities in Africa.

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Introduction

Leopards (*Panthera pardus*) have disappeared from at least 48% of their historic African range (Jacobson et al., 2016) and are increasingly patchily distributed in Africa, having been locally extirpated from areas that have undergone intense habitat conversion or are densely populated by humans (Hunter et al., 2013). This has resulted in elevated conservation attention, and calls for more rigorous research to inform conservation and management decisions (Balme et al., 2014). Of further concern, the majority of leopards in

Africa currently exist outside of parks and reserves (Hunter et al., 2013), and current protected areas alone are insufficient in size to ensure the long-term viability of large carnivore populations (Swanepoel et al., 2013). Improving knowledge on how leopards respond to human presence is therefore necessary to identify habitat requirements and limits of tolerance (Athreya et al., 2013; Balme et al., 2014), and to guide conservation in human-dominated regions (Carter et al., 2015). Presently, however, there have been few such studies, particularly in Africa (but see Henschel et al., 2011), and the limited information available indicates that limits of tolerance are highly regionally specific and likely to change over time (Henschel et al., 2011; Carter et al., 2015). More information is therefore needed from areas with different sources and levels of impact, to inform conservation planning and enable an adaptive management approach to the species' conservation.

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Leopard distribution patterns can also be affected by competition with sympatric large carnivore species (Vanak et al., 2013; Carter et al., 2015), and understanding inter-species interactions between predators can be important for effective conservation planning (Linnell and Strand, 2000; Carter et al., 2015). In many protected areas in Africa, leopards are at risk of kleptoparasitism, injury and direct mortality from lions (*Panthera leo*; Nowell and Jackson, 1996). However, while lions can shape leopard habitat use (Maputla et al., 2015), other studies have found little evidence of spatiotemporal avoidance by leopards (Vanak et al., 2013; Maputla et al., 2015), and uncertainty remains on the nature of these intraguild responses, particularly in human-impacted landscapes.

The goal of this study was to provide information on leopard occurrence, and to identify factors influencing habitat use by leopards, in a disturbed African landscape. Limpopo National Park (LNP) is a legally protected area in Mozambique that is unusual in being inhabited by both leopards and lions as well as by humans and free-grazing livestock. LNP borders on the Kruger National Park (KNP) in South Africa, and is part of the Great Limpopo Transfrontier Park (GLTP) and the wider Greater Limpopo Transfrontier Conservation Area (GLTFCA) (Fig. 1). In this context, a greater understanding of leopard ecological requirements can help conservation practitioners working in a wider matrix of protected areas connected by multiple-use landscapes (Balme et al., 2007; Athreya et al., 2013).

We applied a single-season occupancy modelling framework (MacKenzie et al., 2002) to replicated detection/non-detection camera trap surveys to investigate site use by leopards across a 2500 km² study area in LNP. We then used hierarchical ranking of covariates to assess the relative impacts of environmental, conspecific and anthropogenic variables on leopard site use.

Material and methods

Study area

LNP is a 8238 km² protected area in southern Mozambique, and together with Kruger National Park (KNP), South Africa, and Gonarezhou National Park, Zimbabwe, forms the Greater Limpopo Transfrontier Park (GLTP), part of the Greater Limpopo Transfrontier Conservation Area (GLTFCA), a mosaic of parks and reserves surrounded by areas lacking formal protection (Fig. 1). At the last published estimate, approximately 6500 people inhabited eight villages within the core area of LNP (Fig. 2), and an additional 20,000 people resided in villages along the Limpopo River, the park's eastern boundary (Huggins et al., 2003). Pressures exerted from humans in the park include extensive free-grazing of livestock (including over 20,000 cattle; Stephensen, 2010), land clearing for subsistence agriculture, and 'bushmeat poaching' (Everatt et al., 2014). Bushmeat poaching pressure in the park is high, with modelling of poaching activity suggesting that bushmeat poachers were using circa 80% of LNP in 2013 (Everatt et al., 2014). Poaching techniques employed in the park include the setting of snares and traps, poisonings, and the use of bows and firearms. Recent evidence suggests the establishment of large-scale commercial bushmeat poaching operations in LNP (Everatt and Andresen, unpublished data).

The primary habitat in LNP consists of dry open deciduous tree savanna, or 'sandveld', with deep sandy soils covered predominantly by *Colophospermum mopane* thickets and low open woodlands, as well as seasonally flooded short-grass depressions ('pans'). Rainfall is distinctly seasonal, with 95% of the average 500 mm/year of rainfall occurring between November and April (Stalmans et al., 2004; Cambule et al., 2014). Large mammal populations in LNP were severely affected during the armed conflicts in Mozambique (1964–1974; 1980–1992; Hanks, 2000), and although there is some wildlife recolonisation occurring from neighbouring

KNP, human presence in the park is currently acting as a barrier for the process (Everatt et al., 2014; Lunstrum, 2015). Twenty-two species of ungulate and 18 species of mammalian carnivore occur in the park, including leopards, lions, cheetahs (*Acinonyx jubatus*), spotted hyaenas (*Crocuta crocuta*) and wild dogs (*Lycaon pictus*) (Andresen et al., 2014).

Occupancy survey design

Occupancy models use replicated detection/non-detection surveys to estimate the probability of detecting a species (p), and derive unbiased probabilities of sites being used by the species (Ψ) (MacKenzie et al., 2002). The following assumptions of an occupancy model were initially made: 1) sites are closed to changes in occupancy (i.e. they are either occupied or not by the species for the survey duration); 2) species are not falsely identified; 3) detections are independent; and 4) heterogeneity in occupancy or detection probability are modelled using covariates (MacKenzie et al., 2006). However, given that we employed an approach where the occupancy estimator (Ψ) was interpreted as the probability of site use, rather than the proportion of area occupied (MacKenzie et al., 2006), we were able to relax the closure assumption.

The camera-trap grid covered approximately one third of LNP (circa 2 500 km²). Due to large portions of LNP not being accessible as a result of very limited infrastructure, most sites were located in the central third of the park. Nevertheless, sampling occurred across the major environmental strata of the park, and followed a gradient of the main defining features present in LNP (including habitats, human settlements, drainage lines, and LNP and KNP boundaries) (Fig. 2). Fifty-five sites were sampled over 12 months (November 1, 2011–October 31, 2012).

Data collection

Data were collected through temporally-replicated detection/non-detection 7 day camera trap sampling occasions. A total of 55 stations, each comprised of one digital motion-activated camera with infra-red flash, were employed across a period of 12 months, from November 2011 to October 2012. Camera stations were moved between sites during the survey period, as a result of logistical restrictions. Stations were active for a period ranging between 14 and 219 days (2–30 occasions; mean = 9.9 occasions), and a minimum of 16 stations were deployed at any one time during the survey period. Unequal sampling across sites is accounted for in the modelling process (MacKenzie et al., 2002). In order to maximise the probability of detecting carnivores, cameras were placed along game trails, dirt tracks, waterholes and river edges. Cameras were deployed facing towards the path of movement, and checked regularly for data and malfunctions.

Site use covariates

We identified a total of six prey, sympatric competitor, landscape and anthropogenic covariates to explain heterogeneity in leopard occurrence in LNP (Table 1). For raster-layer based covariates (i.e. proximity to human settlements, proximity to rivers), values were calculated as the mean of all 30 × 30 m pixels included in a 1 km² area around each camera-trap station, located at its centre. Following other authors, we considered this a meaningful scale to investigate the effect of site covariates on habitat selection by a large felid (Sunarto et al., 2012; Everatt et al., 2015; Tan et al., 2017).

Prey resources available to leopards at sites were modelled through the probability of occurrence of a preferred prey species (P) of leopard, impala (*Aepyceros melampus*; Hayward et al., 2006), which is also the most commonly consumed species in contiguous KNP (Bailey, 1993). An impala occupancy model for LNP was

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