Leopard population density across habitats and management strategies in southern Tanzania's Ruaha-Rungwa landscape

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Abstract

Although widely considered one of the most resilient African large carnivores, the status of leopard (*Panthera pardus*) is unknown across much of its remaining African range. We provide the first comparison of leopard population density within different components of a mixed-use landscape in Tanzania, via spatially explicit capture-recapture (SECR) modelling of data from camera trap surveys conducted in the Ruaha-Rungwa landscape in 2018 and 2019. Population density was highest in highly-productive riverine *Acacia*-*Commiphora* habitat in the core tourist area of Ruaha National Park (6.81 ± 1.24 leopards per 100 km^2). The next highest density (4.23 ± 1.02 per 100 km^2) was estimated in similar habitat in the neighbouring MBOMIPA Wildlife Management Area (WMA). Density in the miombo (*Brachystegia*-*Jubelnardia*) woodland-dominated Ikiri block of Rungwa Game Reserve (3.36 ± 1.09 per 100 km^2), a trophy hunting area, was similar to miombo woodland in western Ruaha NP (3.23 ± 1.25 per 100 km^2). Our results illustrate that variation in density across the landscape is likely to be largely driven by differences in prey abundance, itself linked to differences in productivity between habitat types and differences in anthropogenic impacts. Our findings suggest that habitat type and human impacts play a key role in determining density of leopard populations, and that a trophy hunting area with significant protection investment supports a leopard density comparable to that in similar habitat in a photographic tourism area. We also provide evidence that community-managed WMAs have the potential to effectively conserve large carnivore populations at relatively high densities.

1. Introduction

Despite being considered the least threatened subspecies of leopard (*Panthera pardus*; Stein et al., 2016), the African leopard (*Panthera pardus pardus*) has nonetheless lost up to two thirds of its historical range (48-67%; Jacobson et al., 2016). The primary drivers of this decline include the loss and fragmentation of natural habitat (Brink & Eva, 2009) and the decline of many prey species (Craigie et al., 2010). These pressures also increasingly force leopard to use areas occupied by people, which can exacerbate human-leopard conflict, another major threat to the species' survival in Africa (Swanepoel et al., 2015). Although reliable data on trends in leopard status are sorely lacking for sub-Saharan Africa, these combined threats are likely to have caused population declines of at least 30% over the last three generations (Stein et al., 2016).

Nevertheless, the leopard's reputation as one of the most resilient and adaptable African large carnivores has contributed to a relative lack of research and conservation urgency for the species (Balme et al., 2014; Jacobson et al., 2016; Stein et al., 2016). Leopard research to date in Africa has largely been concentrated in areas of lower conservation concern, such as highly protected areas reserved for non-consumptive use, and many efforts have failed to contribute meaningfully to conservation outcomes (Balme et al., 2014). As a result, the status and population trends of leopard across much of its remaining African range is unknown (Jacobson et al., 2016). This lack of empirical population assessments may be contributing to unseen losses for Africa's remaining leopard populations, particularly outside core protected areas (Durant et al., 2016).

Meaningful assessments of a species' status often involve the estimation of population densities or abundances, and are a key requirement to monitor population trends, assess habitat requirements, and select and evaluate appropriate management and conservation strategies (Boitani & Powell, 2012). In particular, estimates of population density allow for comparisons between sites and can be used as a tool to monitor population trends. Spatially explicit capture-recapture (SECR) analysis using camera trap data is a well-established method for estimating population density for marked species (Rovero & Zimmermann, 2016), and is one of the most widely-used and robust methods to assess the status of leopard populations (Jacobson et al., 2016).

Information on leopards in Tanzania is “particularly poor” (Packer, Lichtenfeld, et al., 2009), despite the country being thought to contain approximately 10% of extant African leopard range (Stein et al., 2016). Although several camera trap surveys have been carried out in Tanzania as part of the Tanzania Mammal Atlas Project (Lobora et al., 2008), only three sets of leopard population density estimates have been published for the country, with only two of these employing comparatively statistically-robust methods (Allen et al., 2020; Crosmary et al., 2018; Havmøller et al., 2019).

Tanzania has the largest proportion of land under formal protection of any African country (approximately 48.2%; Riggio et al., 2019), but only around a third of the country’s PAs are designated as National Parks (NPs) or Conservation Areas, where photographic tourism is the only permitted revenue-generating activity (Riggio et al., 2019). In contrast, around two thirds of Tanzania’s PAs are set aside for trophy hunting, with other forms of extractive use permitted alongside this in all except the most strictly-protected hunting areas, Game Reserves (GRs). However, as a result of a lack of population estimates, trophy hunting quotas for leopard in the country are currently largely based on unpublished status assessments (MNRT, 2018). Although trophy hunting has been shown to have the potential to foster conservation of wildlife, particularly large carnivores, with a relatively low ecological footprint (Di Minin et al., 2016; Dickman et al., 2019; Lindsey et al., 2007), it can have strong detrimental impacts on large carnivore populations if carried out unsustainably (Lindsey et al., 2013; Naude et al., 2020; Packer, Kosmala, et al., 2009). Thus, there is a pressing need to assess hunted leopard populations to ensure that quotas are sustainable (Packer et al., 2010; MNRT, 2018).

In addition, the status of many of the country’s hunting areas has been in flux in recent years: while six GRs have been upgraded to NP status since 2018 (including two thirds of Selous GR being upgraded to create Nyerere NP, the largest National Park in East Africa; Kimboy, 2019), a number of lesser-protected areas have been degazetted during this same period (Kideghesho, 2019). Revenue from trophy hunting has also declined in recent years, and there is uncertainty over the long-term economic sustainability of this industry in sub-Saharan Africa (Lindsey et al., 2014). Information on leopard population density is therefore also required to provide insights into the potential impacts these changes may have on the country’s leopard populations, and feed into PA prioritisation exercises.

Finally, in recent years, a growing proportion of the country has been gazetted for community-management as Wildlife Management Areas (WMAs), with 38 existing and planned WMAs set to cover 7% of the country (Keane, 2015). Based on the principles of community-based natural resource management (CBNRM), WMAs are formed from parcels of land set aside for conservation by member villages, and are designed to empower local communities by giving them greater authority over the management of natural resources (WWF, 2014). Communities benefit from participation in WMAs by receiving a share of revenues generated by any wildlife-based enterprises established on the land (normally photographic or trophy hunting tourism; WWF, 2014). However, despite their promise as a means of promoting both long-term protection of wildlife and rural economic development (WWF, 2014), few studies have set out to scientifically assess how effective the WMA initiative has been in meeting its conservation goals (but see Lee, 2018; Lee and Bond, 2018; Kiffner et al., 2020), with a particular research gap across southern Tanzania.

Against this changing conservation landscape, and given Tanzania's potential importance as a stronghold for leopard in sub-Saharan Africa, there is a pressing need to understand the status of the country's leopard populations within the different forms of land use, management strategies, and habitats that make up its PA network. To contribute research to this knowledge gap, we carried out SECR modelling of camera trap data at four sites in the Ruaha-Rungwa landscape in southern Tanzania, including two within different habitats in a National Park, one within an actively-hunted Game Reserve, and one in a community-managed WMA. Our findings provide the first comparison of leopard population density across different habitats and land management strategies within a mixed-use landscape in Tanzania, which has important conservation management implications. Our study also provides one of the first investigations of population status in a leopard population in an African miombo habitat.

2. Methods

2.1. Study area

The study area is situated within the Ruaha-Rungwa landscape, a ~45,000 km^2 mixed-use PA complex in southern Tanzania (Fig. 5.1), recognised by the EU as a Key Landscape for Conservation due to its internationally important wildlife populations (European Commission, 2016).

Ruaha-Rungwa encompasses a spectrum of land management strategies. At its heart lies Ruaha NP, the second largest NP in East Africa at over 20,000 km^2, where only photographic tourism is permitted. To the north of the NP is a complex of three GRs where trophy hunting is permitted: Rungwa, Kizigo, and Muhesi. Neighbouring the park to its east, over the Great Ruaha River, are two community-managed WMAs, the Idodi-Pawaga MBOMIPA WMA and Waga WMA, which act as a buffer between Ruaha NP and the surrounding unprotected village lands. Although both photographic tourism and trophy hunting are permitted in these WMAs, neither activity was taking place at the time of study. A number of other, less-strictly protected areas are also present in the wider landscape. As the PAs in the landscape are unfenced, wildlife often move between these areas and neighbouring non-PAs – particularly large carnivores, whose spatial requirements often cause them to range beyond core PAs (Ripple et al., 2014).

Climate in Ruaha-Rungwa is arid to semi-arid, with average annual rainfall of 600 mm (Fick & Hijmans, 2017), the majority of which falls during a single wet season from December to April (Mtahiko et al., 2006). Vegetation cover in the landscape is a mosaic of Southern *Acacia-Commiphora* bushlands and Central Zambezian miombo (*Brachystegia-Jubelnardia*) woodlands, riverine forests, and flood-plain grasslands.

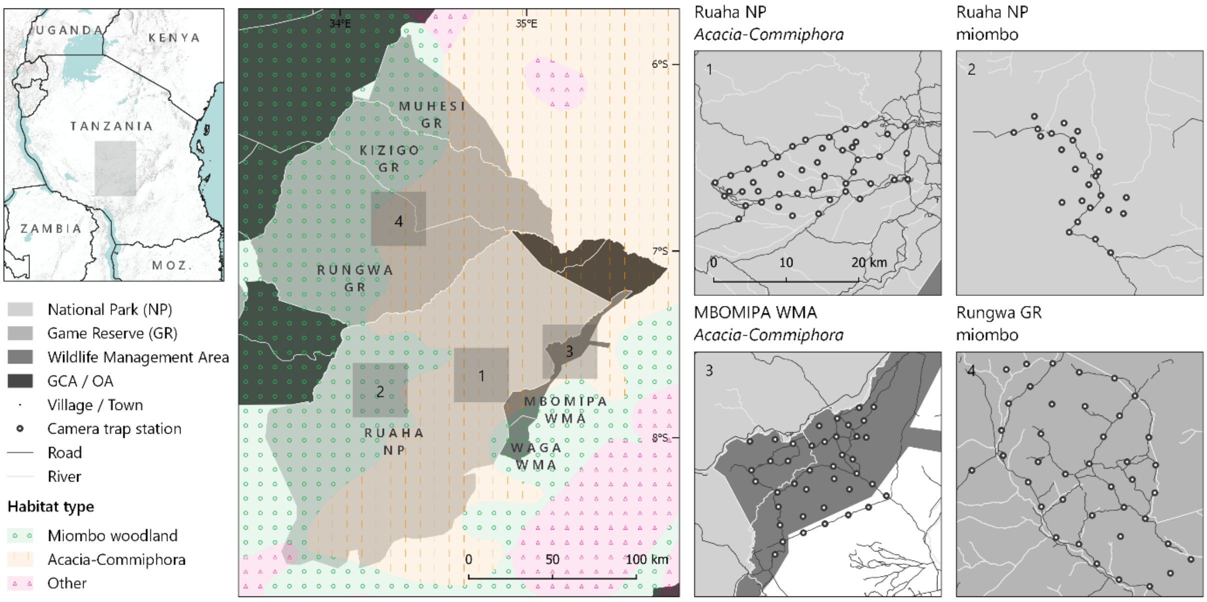

Figure 5.1: Location of the Ruaha-Rungwa landscape within Tanzania; the different land use and habitat types in the study landscape and the location of camera trap survey areas; and detail of camera trap grids in (1) Ruaha NP *Acacia-Commiphora* habitat, (2) Ruaha NP miombo habitat, (3) MBOMIPA WMA *Acacia-Commiphora* habitat, and (4) Rungwa GR miombo habitat.

2.2. Camera trap surveys

We estimated population density using data from camera trap surveys at four sites in the Ruaha-Rungwa landscape, each representing a different habitat and management strategy: the strongly-protected and highly productive core tourist area of Ruaha NP, which is dominated by *Acacia-Commiphora* bushland and open grasslands, and is located near the Great Ruaha River, which exhibits very high herbivore densities as one of the few dry season water sources in the landscape (TAWIRI, 2019); the miombo woodland in western Ruaha NP, which receives less on-the-ground protection than the core tourist area of the NP due to its remoteness and lower tourist traffic; MBOMIPA WMA, a less-strongly protected area of *Acacia-Commiphora* habitat, located in a highly productive area near the Great Ruaha River and receiving a relatively high level of foot patrols in 2018 after several years of absence of law enforcement effort (STEP, 2019), but directly adjacent to unprotected village land; and the Ikiri hunting block of Rungwa GR, an area under strong protection where trophy hunting is permitted and which was actively hunted at the time of data collection, which is dominated by miombo woodland (Fig. 5.1).

2.2.1. Camera set up

We conducted surveys during the dry seasons of 2018 and 2019, using various models of motion-activated camera (Cuddeback Professional Color Model 1347 & X-Change Color Model 1279, Non Typical Inc., Wisconsin, USA; HC500 HyperFire, Reconyx, Wisconsin, USA). The majority of cameras used xenon white flash, to improve the clarity of markings in photos for individual identification. All but one station used paired cameras to maximise the probability of photographing both flanks of animals passing through the station. Cameras were mounted in protective cases and secured with binding wire to prevent damage and loss to both animals and humans. In particularly high-risk areas, cases were further secured with padlocks and camouflaged to reduce the risk of theft.

2.2.2. Survey design

Camera spacing and grid size were set conservatively based on leopard home range data from comparable habitats elsewhere in Africa (e.g. Ray-Brambach et al., 2017), to ensure all individuals in the survey area had a non-zero probability of capture (Noss et al., 2013; Rovero & Zimmermann, 2016). Within this constraint, the spacing of cameras was maximised to ensure that the sampled area exceeded estimated average male home range, as recommended for robust density estimation (Noss et al., 2013; Tobler & Powell, 2013).

We set stations along roads whenever possible, prioritising junctions, to maximise captures of large carnivores, and off-road stations were added along major game trails to avoid gaps in the grid. Cameras were mounted on trees along roads and game trails at a height of 30-40 cm, and checked every 1-4 weeks. Each grid was surveyed for 2-3 months, to ensure sufficient captures without violating the assumption of population closure (Tobler & Powell, 2013).

2.2.3. Survey grids

Forty-five stations (all but one paired; 89 cameras) were deployed over an area of 223 km^2 (average spacing 1.96 km) in the core tourist area of Ruaha NP, for 83 days between June and September 2018.

Twenty-six stations (all paired; 52 cameras) were deployed in the miombo woodland of Ruaha NP, covering an area of 152 km^2 (average spacing 1.88 km), for 90 days between August and November 2018.

Forty stations (all paired; 80 cameras) were deployed across 270 km^2 (average spacing 2.08 km) in MBOMIPA WMA, for 70 days between September and November 2018.

Forty stations (all paired; 80 cameras) were deployed over an area of 555 km^2 (average spacing 3.46 km) in the Ikiri block of Rungwa GR, for 90 days between July and October 2019.

Detailed summary information for the four survey grids can be found in S5.1.

2.3. Density estimation

We estimated population density of leopard (defined as the number of adult individuals per 100 km^2) at each site via maximum-likelihood SECR analysis (Efford, 2011), using package *secr* version 3.2.1 (Efford, 2019a) in R version 3.6.2 (R Core Team, 2017) and RStudio version 1.2.5033 (RStudio Team, 2020).

Following data collection, individual leopards were identified from camera trap photos via visual inspection of their unique pelage patterns and sexed based on visible external genitalia (Tobler & Powell, 2013), with IDs verified by a second observer; photos in which individuals could not be confidently identified were excluded from analysis. Data inputs for each grid consisted of a capture history detailing the location and sampling occasion of captures for each individual, using the flank with the greatest number of captures for each grid, and the trap layout, containing information on the location and activity of each camera station. Sampling occasions were defined as a 24 hour period running from midday to midday, as recommended for nocturnal species (Rovero & Zimmermann, 2016). See S5.2 for additional details on the SECR modelling process.

2.4. Model selection

We included station location (on- or off-road) as a covariate hypothesised to influence capture probability (g0), to account for the fact that capture probabilities are likely to be higher at stations located on roads (which are often used preferentially by large carnivores; McKenzie et al., 2012) than on trails. We included sex as a covariate hypothesised to influence both capture probability (g0) and the movement parameter (σ), as large felids are known to exhibit sex-specific traits in their ranging behaviours (Tobler & Powell, 2013). Sex was modelled as a covariate by fitting a hybrid mixture model, which allows the inclusion of individuals of unknown sex by applying a random effect to individuals in this category (Efford, 2019b).

We fitted eight models to estimate population density and test the influence of camera location and sex on model parameters (see S5.3). Models were ranked based on their Akaike Information Criterion score, corrected for small sample size (AICc). Where more than one model had substantial empirical support ($\Delta AICc < 2$; Burnham and Anderson, 2004), we used model averaging to determine the final population density and parameter estimates for that grid. The width of the buffer around each trapping grid was increased until density estimates stabilised, to ensure that individuals whose home range centre was located outside the buffer had a negligible chance of being detected (Efford, 2020).

2.5. Precision of estimates

To assess the precision of our population density estimates, we calculated the half relative confidence interval width (HRCIW) for each grid, using the equation: $HRCIW = \frac{0.5 \times (UCL - LCL)}{Density} \times 100$, where UCL and LCL are the upper and lower 95% confidence limits of the density estimate for that grid, respectively (Dröge et al., 2020). HRCIW provides a measure of the magnitude of population change that an estimate has a reasonable probability of detecting.

3. Results

3.1. Survey effort

Across the four study sites, a total sampling effort of 11,668 camera trap nights across 151 stations yielded 925 images of leopard, 95.2% of which were suitable for individual identification (see S5.1). Counting only the flank with the greatest number of captures for each grid resulted in a total of 362 unique capture events, from which 90 individuals were identified. 73.0% of identified individuals were recaptured at more than one station in the Ruaha NP *Acacia-Commiphora* grid, versus 66.7% in the Ruaha NP miombo grid, 50.0% in the MBOMIPA WMA grid, and 26.3% in the Rungwa GR grid.

Sex was confidently assigned to 83.8% of individuals identified in the Ruaha NP *Acacia-Commiphora* grid (15 female, 16 male, 6 unknown), 83.3% of individuals in the Ruaha NP miombo grid (7 female, 3 male, 2 unknown), 77.3% of individuals in the MBOMIPA WMA grid (8 female, 9 male, 5 unknown), and only 47.4% of individuals in the Rungwa GR grid (4 female, 5 male, 10 unknown). The lower rates of recapture and sex identification in the Rungwa GR grid were likely a result of wider spacing between stations.

3.2. Population density

We estimated density based on left flank captures for the Ruaha NP *Acacia-Commiphora*, MBOMIPA WMA, and Rungwa GR grids, and from right flank captures for the Ruaha NP miombo grid. Buffer width stabilised at 12 km for the Ruaha NP *Acacia-Commiphora* grid, 14 km for the MBOMIPA WMA grid, 16 km for the Rungwa GR grid, and 30 km for the Ruaha NP miombo grid.

The top-ranked model of population density was secr.road.sex.s (g0 varies with station location; σ varies with sex) for the Ruaha NP *Acacia-Commiphora* grid, and secr.sex.s (σ varies with sex) for the Ruaha NP miombo grid, in each case being the only model with substantial support. For both MBOMIPA WMA and Rungwa GR grids, there were two models of density with substantial support (ΔAICc < 2): secr.road.sex.s and secr.sex.s in MBOMIPA WMA, and secr.0 (null model) and secr.sex.s in Rungwa GR. Results of model ranking for all sites can be found in S5.3. Sex therefore had a significant impact on leopard movement across all four sites, while camera location influenced capture probabilities in the two *Acacia-Commiphora* sites.

We estimated the highest population density in the Ruaha NP *Acacia-Commiphora* grid, at 6.81 ± 1.24 leopards per 100 km^2. The next highest density of 4.23 ± 1.02 individuals per 100 km^2 was estimated for the *Acacia-Commiphora* MBOMIPA WMA grid, followed by 3.36 ± 1.09 per 100 km^2 in the miombo-dominated Ikiri block of Rungwa GR, and 3.23 ± 1.25 per 100 km^2 in the miombo of Ruaha NP (Table 5.1; Fig. 5.2).

A HRCIW of 50% or lower indicates that a density estimate has a reasonable probability of detecting a critical population decline of 50%, thus meeting the IUCN A2 criterion to classify a leopard population as *Endangered* if that decline takes place within 10 years or 3 generations (whichever is longer; IUCN, 2019; Dröge et al., 2020). The density estimates from the Ruaha NP *Acacia-Commiphora* grid (HRCIW = 36.1%) and MBOMIPA WMA (48.3%) were sufficiently precise to fall below this threshold, but the estimates from miombo woodland in Rungwa GR (65.6%) and Ruaha NP (80.2%) were not (Table 5.1).

Table 5.1: Population density and parameter estimates for the four survey sites. Estimates taken from models with substantial empirical support (ΔAICc < 2); where more than one model had substantial support, model averaging was used to obtain averaged estimates.

Parameter	Estimate	**Ruaha NP**[1] *Acacia-Commiphora*	**Ruaha NP**[2] miombo	**MBOMIPA WMA**[3] *Acacia-Commiphora*	**Rungwa GR**[4] miombo
g0[5]	Mean ± SE		0.015 ± 0.006		0.007 ± 0.003
	95% CI		0.007 – 0.033		0.003 – 0.015
$g0_{on\text{-}road}$[5]	Mean ± SE	0.035 ± 0.004		0.022 ± 0.004	
	95% CI	0.028 – 0.044		0.015 – 0.032	
$g0_{off\text{-}road}$[5]	Mean ± SE	0.003 ± 0.002		0.013 ± 0.005	
	95% CI	0.001 – 0.011		0.006 – 0.029	
σ_{female}[6]	Mean ± SE	1532 ± 109	1964 ± 377	1865 ± 190	2321 ± 594
	95% CI	1333 – 1761	1352 – 2852	1529 – 2276	1416 – 3804
σ_{male}[6]	Mean ± SE	3211 ± 215	12964 ± 3663	3521 ± 482	2868 ± 537
	95% CI	2816 – 3661	7530 – 22318	2696 – 4599	1992 – 4128
Density[7]	Mean ± SE	**6.81 ± 1.24**	**3.23 ± 1.25**	**4.23 ± 1.02**	**3.36 ± 1.09**
	95% CI	4.78 – 9.70	1.55 – 6.73	2.65 – 6.74	1.82 – 6.23
HRCIW (%)[8]		36.1	80.2	48.3	65.6

[1] Parameter estimates from only model with strong support (ΔAICc < 2); secr.road.sex.s

[2] Parameter estimates from only model with strong support; secr.sex.s

[3] Averaged parameter estimates from models with strong support; secr.road.sex.s and secr.sex.s

[4] Averaged parameter estimates from models with strong support; secr.0 and secr.sex.s

[5] g0 = capture probability at home range centre

[6] σ = distance parameter related to home range size

[7] Population density defined as the number of individuals per 100 km^2

[8] HRCIW = half relative confidence interval width; a measure of the magnitude of population change that could be confidently detected

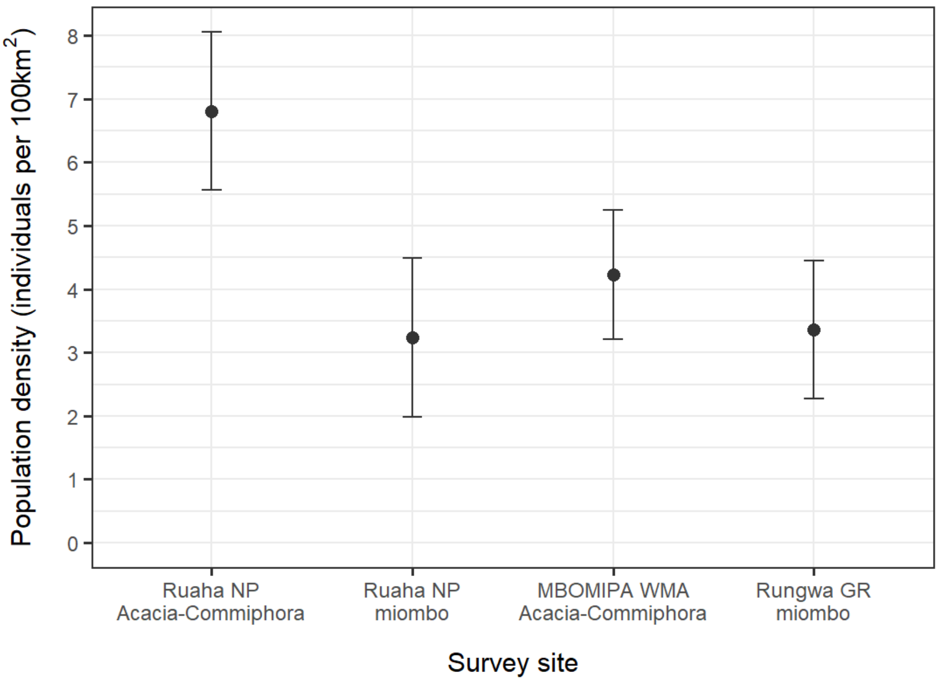

Figure 5.2: Population density estimates for the four survey sites, with error bars showing the standard error (SE) for each estimate.

4. Discussion

This study provides evidence of a globally-important leopard population in the Ruaha-Rungwa landscape of southern Tanzania. We estimated a high population density for leopard in the riverine core tourist area of Ruaha NP, with slightly lower densities estimated for neighbouring MBOMIPA WMA and the miombo woodland of Rungwa GR and Ruaha NP. These are some of the first such estimates for the country (but see Allen et al., 2020; Havmøller et al., 2019), including one of the first robust estimates of leopard population density in a trophy hunting area in Tanzania, and also provide one of the first insights into leopard ecology in a miombo woodland habitat (but see Davis et al., 2020; Jorge, 2012).

While the density estimates for the core tourist area of Ruaha NP and MBOMIPA WMA are sufficiently precise to detect a critical population decline per IUCN guidelines, neither density estimate from the miombo woodland sites meets this threshold, indicating that caution should be exercised when using these estimates as a baseline for population monitoring. However, future surveys at the same sites could nonetheless provide valuable information on mortality by comparing the individuals captured across years.

Our estimates of leopard population density are comparable to densities estimated using SECR methods elsewhere in Africa, which range from 0.76 leopards per 100 km^2 in South Africa's Little Karoo (Mann, 2014) to 14.51 per 100 km^2 in Namibia's fenced Okonjima Nature Reserve (Noack et al., 2019). Looking specifically to Tanzania, our estimates are consistent with the range of leopard densities estimated using comparable methods in the Udzungwa Mountains (2-8 per 100 km^2; Havmøller et al., 2019), while our estimate for the core tourist area of Ruaha NP is higher than the dry season density estimated in the similarly highly-protected Serengeti NP (5.41 per 100 km^2; Allen et al., 2020). The densities we estimated in miombo woodland are comparable to densities estimated in the Eastern miombo woodland of Niassa National Reserve, Mozambique (2.18-4.31 per 100 km^2; Jorge, 2012), and are higher than the mean density estimated in the human-impacted Central Zambezian miombo woodland of Kasungu NP, Malawi (1.9 per 100 km^2; Davis et al., 2020).

4.1. Drivers of variation in density

The high population density we estimated in the core tourist area of Ruaha NP is likely to be primarily a result of this area's position near the highly-productive Great Ruaha River, which supports the highest dry season ungulate biomass across the landscape (TAWIRI, 2019). This is further supported by the relative abundance of leopard prey species (measured by Relative Abundance Index (RAI), see S5.4; O'Brien, 2011), which was highest in this study site (ΣRAI = 101.1), followed by MBOMIPA WMA (70.8), Rungwa GR (63.1), and Ruaha NP miombo (38.5). This aligns with studies elsewhere in Africa that have found prey abundance to be an important predictor of leopard population density (Marker & Dickman, 2005; Stein et al., 2011; Boast & Houser, 2012; Rosenblatt et al., 2016).

Despite having comparable highly-productive habitat to the core tourist area of Ruaha NP, MBOMIPA WMA currently supports a lower density of leopard in the area surveyed. This is likely to be largely a result of the higher level of anthropogenic impacts faced by wildlife in this area as a result of its proximity to unprotected village land. Nine illegal incursions (two picturing captured bushmeat) were photographed in the WMA during the survey period, versus two in Rungwa GR, one in Ruaha NP miombo, and none in the core tourist area of Ruaha NP. Accordingly, while still relatively high, the relative abundance of many leopard prey species was lower in MBOMIPA WMA than in the core tourist area of Ruaha NP (S5.4). In addition to impacting prey populations, bushmeat poaching may also be having a direct impact on leopard, as snaring has been shown to directly contribute to leopard mortality in Africa (Swanepoel et al., 2015), including in the study landscape (Ruaha Carnivore Project, unpublished data). Furthermore, leopards in MBOMIPA WMA are likely to be subject to a strong edge effect (Balme et al., 2010), as habitat is highly degraded in unprotected lands beyond the WMA's south-eastern boundary (Abade et al., 2018). This may be further exacerbated by the high levels of human-leopard conflict reported in the area (Dickman et al., 2014). Similar negative relationships between leopard population density and human encroachment around PAs have been identified elsewhere in Africa (Balme et al., 2010; Havmøller et al., 2019; Henschel et al., 2011; Marker & Dickman, 2005; Rosenblatt et al., 2016).

The lower leopard population density in both miombo woodland sites is likely to be a result of the lower abundance of prey supported by miombo woodlands, due to naturally low soil productivity of this habitat (Frost, 1996). This is corroborated by our RAI estimates (S5.4), and mirrors findings from miombo woodlands in northern Mozambique (Jorge, 2012). In Rungwa GR, leopard population density was very similar to the comparable miombo habitat of Ruaha NP, despite the site in Rungwa GR supporting higher relative abundances of many leopard prey species (S5.4). This suggests that, although the Ikiri block of Rungwa GR currently supports a comparable leopard population density, direct mortality through trophy hunting offtake may be playing a role in keeping leopard below potential densities in the GR. However, comparisons between density estimates for these sites should be made with caution, given their relatively low precision.

4.2. Trophy hunting areas and sustainable quotas

Our study provides the first published spatially explicit population density estimate for a trophy-hunted leopard population in Tanzania. Such robust estimates of population densities are particularly important in trophy hunting areas, to form the basis of sustainable hunting quotas (Strampelli et al., 2018).

Although wildlife authorities in Tanzania strive to base leopard hunting quotas on robust, empirical population data, they are currently limited by the lack of information available for the country's leopard populations (TAWIRI, 2009; MNRT, 2018).

At present, leopard quotas in Tanzania are based on a national population estimate extrapolated from average densities of 7.9 per 100 km^2 for NPs and 4.5 per 100 km^2 for GRs, largely derived from unpublished camera trap studies (MNRT, 2018). While Tanzania's Ministry of Natural Resources & Tourism (MNRT) administer block-specific hunting quotas, the lack of density estimates for the majority of Tanzania's hunting areas means that these often cannot be based on information specific to the population of interest. The figures currently employed are higher than our estimated population densities for Ruaha NP and Rungwa GR, respectively, which are each the second largest PA of their type in Tanzania. Although the average estimate used for WMAs is, at 2.3 per 100 km^2, lower than our estimate for MBOMIPA WMA, this figure also applies to GCAs, where human settlement and livestock grazing are unrestricted and leopard densities are therefore likely to be lower. Our density estimate from MBOMIPA WMA was also from the best protected and most productive part of a WMA which forms a boundary along a major river, so is likely to support higher wildlife densities than many other WMAs across the country. As a result, we encourage our estimates to be employed alongside existing population estimates from elsewhere in the country to inform conservation policy.

Although our results indicate that the leopard population in the Ikiri block of Rungwa GR may be below its potential carrying capacity (as found for many large carnivore populations in hunting areas across Africa; see Chapman & Balme, 2010; Loveridge, Valeix, Chapron, et al., 2016; Packer et al., 2010), they also suggest that this trophy hunting area supports a leopard population comparable to that in similar habitat in a photographic tourism area in adjacent Ruaha NP. Our findings are likely a result of the substantial management investment received in the Ikiri block over the last four years, particularly in the form of frequent ground and law enforcement patrols, investment in roads and infrastructure, and ranger training support (STEP, 2019). We therefore caution against extrapolating these findings to other areas, and instead encourage additional block-specific surveys, especially in hunting blocks not receiving comparable levels of protection investment or those that border unprotected village land.

4.3. Insights into effectiveness of CBNRM in Tanzania

We provide evidence that MBOMIPA WMA is an important area of habitat for leopard and its prey species in the Ruaha-Rungwa landscape, acting as a buffer zone between Ruaha NP and the surrounding unprotected village lands, where intense human activities and human-induced mortality are a key limiting factor to leopard distribution (Abade et al., 2018). The WMA is particularly important for wildlife in the wider landscape as it lies along the Great Ruaha River, thus protecting one of the few sources of dry season surface water in the landscape. However, this area may be acting as an attractive sink, drawing wildlife from the adjoining area of strong protection and good habitat to an area with higher mortality risk (Loveridge, Valeix, Elliot, et al., 2016). Nevertheless, our results suggest that WMAs have the potential to effectively conserve large carnivore populations at relatively high densities.

Like MBOMIPA, many of Tanzania's WMAs and other forms of lesser-protected areas are positioned along the boundaries of strongly-protected areas (WWF, 2014). As such, these areas not only play an important role on a local scale, insulating highly-protected areas from illegal activities and other anthropogenic impacts, but may also act as stepping-stones linking multiple strongly-protected areas on a national scale. These areas are therefore critical to many of the country's potential wildlife corridors (Riggio & Caro, 2017). However, despite their potential to contribute to conservation goals, the country's WMAs appear to have achieved mixed success in their engagement of local communities (Walsh, 2000), and there is no clear evidence of the initiative contributing to widespread poverty reduction (Keane et al., 2020).

4.4. Conservation recommendations

The level of variation in our density estimates illustrates the importance of surveying different components of a landscape, and not extrapolating density estimates from a single study site (Foster & Harmsen, 2012). This is particularly important as there is a general bias in density studies towards selecting survey sites in areas thought to support higher densities of the target species (Suryawanshi et al., 2019). We therefore recommend that future studies of leopard in Ruaha-Rungwa complement our findings by assessing population status in the landscape's more marginal zones, such as vacant or less-protected hunting blocks and completely unprotected land, or less productive areas, to provide a more complete view of leopard status across the landscape.

Given the apparent importance of prey abundance in shaping leopard population density, our findings support recommendations that securing prey populations should be a priority for the conservation of African leopard populations (Rosenblatt et al., 2016; Searle et al., 2020). Conservation efforts should also prioritise investments aimed at reducing bushmeat poaching and other human impacts in areas adjacent to unprotected land.

We recommend that our results be employed to inform sustainable use management in the Ikiri block of Rungwa GR, and encourage the research and hunting communities to collaborate on similar monitoring efforts for hunting areas elsewhere in Tanzania, to equip policymakers with the information required to set sustainable levels of offtake. Given that hunting areas comprise a significant portion of leopard range in Tanzania (MNRT, 2018), we recommend the continued implementation of regulations that have been shown to improve sustainability of trophy hunting and reduce long-term risk of extinction of hunted leopard populations, such as minimum age and size requirements for hunted individuals (Balme et al., 2012; Braczkowski et al., 2015), and continued investment in protection in hunting areas. For areas where trophy hunting is judged to not be a viable land-use option for the long-term, these regulations should be implemented until alternative, conservation-oriented land use strategies can be put in place (Di Minin et al., 2016; Dickman et al., 2019). As law enforcement in many of Tanzania's hunting areas is currently funded almost exclusively through hunting revenues (MNRT, 2018), phasing out trophy hunting without viable alternative financing or forms of land use already in place risks undermining resources for protection of vital wildlife habitat.

Finally, given the potentially important role of many WMAs in maintaining healthy ecosystems across Tanzania, as well as their potential contributions to local development, we suggest that continued and increased support for WMAs be considered a national and international conservation priority, with particular efforts made to empower participating communities and secure the initiative's intended development benefits. We recommend the implementation of long-term wildlife monitoring in WMAs like MBOMIPA, which are adjacent to highly-protected areas, to assess trends in wildlife populations and identify possible population sinks. MBOMIPA WMA in particular should be prioritised for additional investment and support, to safeguard its position as a critical buffer for the globally-important wildlife populations of Ruaha-Rungwa.

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Supplementary Material

S5.1 Survey grid summary information

S5.2 Additional details on the SECR modelling process

S5.3 Results of model ranking

S5.4 Preferred prey relative abundance indices (RAI)

S5.1 Survey grid summary information

Table S5.1.1: Summary information for the four survey grids in Ruaha-Rungwa.

	Ruaha NP *Acacia-Commiphora*	Ruaha NP miombo	MBOMIPA WMA *Acacia-Commiphora*	Rungwa GR miombo
Survey duration (nights)	83	90	70	90
Stations	45	26	40	40
Trap nights	3,601	2,187	2,689	3,191
Average spacing	1.96 km	1.88 km	2.08 km	3.46 km
Survey area[1]	223 km^2	152 km^2	270 km^2	555 km^2
Buffer width	12 km	30 km	14 km	16 km
Flank with most captures	Left	Right	Left	Left
Individuals recorded[2]	37	12	22	19
Female	15	7	8	4
Male	16	3	9	5
Sex unknown	6	2	5	10
Capture events[2]	201	44	85	32
Recapture rate[2,3]	73.0%	66.7%	50.0%	26.3%

[1] Area of the minimum convex polygon around all stations (does not include buffer)

[2] Based on the flank with most captures for each grid

[3] Percentage of identified individuals recaptured at more than one station during the survey period

S5.2 Additional details on the SECR modelling process

As camera traps do not physically capture animals, we classed stations as proximity detectors, which act independently of one another. Detection probability was modelled using a half-normal detection function, which describes the probability of capture (P) of individual i at trap j as a decreasing function with distance (d) from that individual's home range centre: $Pij = g0\exp(-dij^2/2\sigma^2)$, where g0 is the capture probability at the home range centre, and σ is a distance parameter related to home range size (Efford, 2004).

In line with previous studies (Royle et al., 2009), we fitted a Bernoulli encounter model; under this model, an individual can only be captured at most once at a single station on any sampling occasion (as multiple visits to a single station on the same night are unlikely to be independent), but can be captured at more than one station within a single sampling occasion. The width of the buffer around each trapping grid was increased until density estimates stabilised, to ensure that individuals whose home range centre was located outside the buffer had a negligible chance of being detected (Efford, 2020).

S5.3 Results of model ranking

Table S5.3.1: Model ranking of leopard density models for the four survey sites in Ruaha-Rungwa, based on AIC corrected for small sample size, AICc. Rows shaded grey indicate models with substantial empirical support (ΔAICc < 2 from the top-ranked model).

Model[1]	nPar	LogLik	AICc	ΔAICc	AICc Wt
Ruaha NP – *Acacia-Commiphora*					
secr.road.sex.s	6	-1135.938	2286.675	0.0000	0.8084
secr.road.sex	7	-1135.846	2289.554	2.8790	0.1916
secr.sex.s	5	-1150.683	2313.302	26.6270	0.0000
secr.sex	6	-1150.639	2316.078	29.4030	0.0000
secr.road.sex.g	6	-1155.316	2325.433	38.7580	0.0000
secr.road	5	-1160.210	2332.355	45.6800	0.0000
secr.sex.g	5	-1171.889	2355.713	69.0380	0.0000
secr.0	4	-1176.064	2361.378	74.7030	0.0000
Ruaha NP – miombo					
secr.sex.s	5	-284.223	588.446	0.0000	0.9574
secr.road.sex.s	6	-283.375	595.551	7.1050	0.0274
secr.sex	6	-283.965	596.730	8.2840	0.0152
secr.0	4	-293.380	600.475	12.0290	0.0000
secr.road	5	-292.787	605.574	17.1280	0.0000
secr.sex.g	5	-293.129	606.258	17.8120	0.0000
secr.road.sex	7	-283.044	608.088	19.6420	0.0000
secr.road.sex.g	6	-292.361	613.522	25.0760	0.0000
MBOMIPA WMA – *Acacia-Commiphora*					
secr.road.sex.s	6	-522.214	1062.029	0.0000	0.5937
secr.sex.s	5	-524.877	1063.503	1.4740	0.2841
secr.road.sex	7	-522.065	1066.129	4.1000	0.0764
secr.sex	6	-524.779	1067.157	5.1280	0.0457
secr.road	5	-530.902	1075.553	13.5240	0.0000
secr.road.sex.g	6	-529.338	1076.276	14.2470	0.0000
secr.sex.g	5	-532.613	1078.976	16.9470	0.0000
secr.0	4	-534.380	1079.114	17.0850	0.0000
Rungwa GR – miombo					
secr.0	4	-218.094	447.046	0.0000	0.4176
secr.sex.s	5	-216.491	447.597	0.5510	0.3171
secr.sex	6	-215.575	450.150	3.1040	0.0885
secr.sex.g	5	-218.094	450.804	3.7580	0.0638
secr.road	5	-218.094	450.804	3.7580	0.0638
secr.road.sex.s	6	-216.489	451.979	4.9330	0.0355
secr.road.sex.g	6	-218.094	455.189	8.1430	0.0071
secr.road.sex	7	-215.570	455.323	8.2770	0.0067

[1] secr.0 = null model

secr.sex = σ and g0 vary with sex

secr.sex.s = σ varies with sex

secr.sex,g = g0 varies with sex

secr.road = g0 varies with station location (on- or off-road)

secr.road.sex = g0 varies with station location and sex; σ varies with sex

secr.road.sex.s = g0 varies with station location; σ varies with sex

secr.road.sex,g = g0 varies with station location and sex

S5.4 Preferred prey relative abundance indices (RAI)

Relative species abundance is a component of biodiversity, and refers to how common or rare a species is relative to other species in a defined community (O'Brien, 2011). The relative abundance index (RAI) of all leopard preferred prey species was calculated from the 2018 and 2019 CT data to provide a measure of prey availability for each study site. Mammal species were classified as preferred prey based on the preferred prey body size range and known dietary preferences of leopard (Hayward et al., 2006).

RAI was calculated by multiplying the number of capture events for a given species in each grid by 100, and dividing this by the number of trap nights for that grid (Rovero & Zimmermann, 2016). Capture events were defined as captures taking place more than 30 minutes after the previous capture of that species at the same station.

While RAI is limited by its inability to account for imperfect and variable detection (particularly as our camera locations were optimised for captures of carnivores, and were thus not optimised for ungulates; Sollmann et al., 2013), these issues are somewhat mitigated by the fact that we are comparing similar species across grids of similar design.

Table S5.4.1: Relative abundance indices (RAI) for leopard preferred prey species in Ruaha-Rungwa, based on data from the 2018 and 2019 camera trap surveys.

		Relative Abundance Index (RAI)			
Common name	Latin name	Ruaha NP *Acacia-Commiphora*	Ruaha NP miombo	MBOMIPA WMA *Acacia-Commiphora*	Rungwa GR miombo
African savanna hare	*Lepus victoriae*	1.5	4.5	0.0	0.0
Bush duiker	*Sylvicapra grimmia*	1.7	8.0	6.7	36.4
Bushpig	*Potamochoerus larvatus*	1.7	2.2	1.3	0.2
Bushbuck	*Tragelaphus scriptus*	0.0	0.2	0.3	0.1
Common warthog	*Phacochoerus africanus*	7.9	17.6	2.8	12.0
Impala	*Aepyceros melampus*	74.6	0.2	44.9	1.1
Kirk's dik-dik	*Madoqua kirkii*	12.2	0.3	4.6	7.7
Klipspringer	*Oreotragus oreotragus*	0.0	0.0	0.0	0.0
Lesser kudu	*Tragelaphus imberbis*	1.5	0.0	10.0	0.0
Natal red duiker	*Cephalophus natalensis*	0.0	0.0	0.3	0.0
Oribi	*Ourebia ourebi*	0.0	1.6	0.0	3.4
Sharpe's grysbok	*Raphicerus sharpei*	0.0	2.7	0.0	0.4
Southern reedbuck	*Redunca arundinum*	0.0	1.1	0.0	1.7
	Total	101.1	38.5	70.8	63.1

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