Leopard population density varies across habitats and management strategies in a mixed-use Tanzanian landscape

Abstract

With large carnivores undergoing widespread range contractions across Africa, effective monitoring across mixed-use landscapes should be considered a priority to identify at-risk populations and prioritise conservation actions. 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 camera trap data from the Ruaha-Rungwa landscape in 2018 and 2019. Population density was highest in highly-productive *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 a neighbouring community-managed area (MBOMIPA WMA). Lowest densities were estimated in miombo (*Brachystegia-Jubelnardia*) woodland habitat, both in a trophy hunting area (Rungwa Game Reserve; 3.36 ± 1.09 per 100 km^2) and inside the National Park (3.23 ± 1.25 per 100 km^2). Population density was highly correlated with prey abundance, suggesting that variation in leopard density may be primarily driven by availability of prey, which likely varies with habitat types and anthropogenic impacts. Anthropogenic mortality may also have a direct influence on leopard in more impacted areas, but further research is required to investigate this. Our findings show that a hunting area with significant protection investment supports a leopard density comparable to similar habitat in a photographic tourism area. We also provide evidence that community-managed areas have the potential to effectively conserve large carnivore populations at relatively high densities, but may be vulnerable to edge effects.

1. Introduction

Protected areas (PAs) across sub-Saharan Africa are becoming increasingly isolated as a result of human pressures (Newmark, 2008), and many have failed to mitigate human-induced threats to mammal populations (Craigie et al., 2010). As such, the continued protection of the continent's wildlife populations remains precarious. The African conservation landscape is also undergoing widespread changes, including the decline of trophy hunting in parts of the continent (Lindsey et al., 2014) and the growth of landscape-scale and development-linked strategies (Hackel, 1999; Suich et al., 2009). However, many of these changes are being implemented without sufficient information on the impacts of different conservation models on biodiversity and ecosystem function (UNEP-WCMC et al., 2018). Faced by a chronic lack of funding for conservation (Lindsey et al., 2018), there is a pressing need to assess how species are faring across the land use types in place on the continent, to help inform and prioritise conservation strategies (Coetzee, 2017).

Large carnivores are widely considered to be high-priority species for monitoring, as their loss can have profound consequences for the structure and function of ecosystems (Ripple et al., 2014). These species are also particularly susceptible to habitat loss and persecution, as individuals roam widely across ranges that can extend beyond the borders of protected areas (Ripple et al., 2014). Inside these fragmented landscapes, carnivores are exposed to high levels of mortality (Woodroffe, 2000), often due to accidental or intentional killing by humans (Balme et al., 2009; Loveridge et al., 2007). As a result, large carnivore populations are highly vulnerable to population sinks surrounding PA boundaries, which can contribute to edge effects that reverberate through populations within protected areas (Woodroffe and Ginsberg, 1998). With large carnivores undergoing widespread range contractions across the African continent (Wolf & Ripple, 2016), effective monitoring of key measures of status, such as population densities, should be considered a priority to help identify at-risk populations.

Despite being considered one of Africa's most resilient large carnivores, the leopard (*Panthera pardus*; Stein et al., 2016) has lost up to two thirds of its historical range on the continent (48-67%; Jacobson et al., 2016). A relative lack of conservation urgency for the species has resulted in research efforts being largely concentrated in areas of lower conservation concern, such as highly protected areas reserved for non-consumptive use (Balme et al., 2014; Stein et al., 2016). As a result, the status and population trends of leopard is unknown across much of its remaining African range (Jacobson et al., 2016).

Although Tanzania is thought to contain approximately 10% of extant African leopard range (Stein et al., 2016), information on the country's leopards is considered particularly poor (Packer et al., 2009), with only three sets of population density estimates published for the country (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), around two thirds of which are set aside for trophy hunting. However, as a result of the country's lack of population estimates, trophy hunting quotas for leopard are currently largely based on unpublished status assessments (MNRT, 2018). The status of many of the country's hunting areas has also been in flux in recent years: while six trophy hunting areas have been upgraded to National Park status since 2018 (Kimboy, 2019), a number of lesser-protected trophy hunting areas have been degazetted during this same period (Kideghesho, 2019).

At the same time, a growing proportion of the country has been gazetted for community-management as Wildlife Management Areas (WMAs; Keane, 2015), which are designed to empower local communities to have greater authority over the management of natural resources, and benefit from revenues generated by wildlife-based enterprises on their land (normally photographic or trophy hunting tourism; WWF, 2014). However, despite its promise as a means of promoting both long-term protection of wildlife and rural economic development (WWF, 2014), few studies have set out to assess how effective this initiative has been in meeting its conservation goals, 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 – the country's leopard populations should be assessed under the different forms of land use, management strategies, and habitats that make up its PA network, to improve our understanding of the potential impacts these changes may have on the species. The country also provides a representative case study of many conservation landscapes across Africa, where trophy hunting is a major funding mechanism alongside photographic tourism (Lindsey et al., 2007), and community-management is an increasingly prominent land management framework.

In this study, we carried out spatially explicit capture-recapture (SECR) modelling of camera trap data to estimate leopard population density at four sites in southern Tanzania's Ruaha-Rungwa landscape, including two within different habitats in a National Park, one within a trophy hunting area, and one in a community-managed area. We expected leopard density to be highest in the National Park and lower in the community-managed area, despite its comparable habitat, as a result of edge effects (Abade et al., 2018; Balme et al., 2010). We expected lower densities in the miombo woodland sites within the National Park and trophy hunting area due to lower habitat productivity (Frost, 1996), possibly with lower densities in the hunting area as a result of hunting offtake (Packer et al., 2010). Together, our findings provide the first comparison of leopard status across different habitats and land management strategies within a mixed-use landscape in Tanzania, and have important implications for conservation management.

2. Methods

2.1. Study area

The study area was situated within the Ruaha-Rungwa landscape, a ~45,000 km^2 mixed-use PA complex in southern Tanzania (Fig. 1), which is recognised by the EU as a Key Landscape for Conservation (European Commission, 2016). Ruaha-Rungwa encompasses a spectrum of land management strategies. At its heart lies the ~20,000 km^2 Ruaha National Park, where only photographic tourism is permitted. To the north of the National Park are Rungwa, Kizigo, and Muhesi Game Reserves, where trophy hunting is permitted. Neighbouring the National 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 the National Park and surrounding unprotected village lands. Although both photographic tourism and trophy hunting are permitted in these community-managed areas, 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 (Fig. 1). As the PAs in the landscape are unfenced, wildlife often move between these areas and neighbouring non-PAs.

Climate in Ruaha-Rungwa is arid to semi-arid, with average annual rainfall of 600 mm (Fick and 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.

2.2. Camera trap surveys

We estimated population density from camera trap surveys at four sites in the Ruaha-Rungwa landscape, each representing a different habitat and management strategy (Fig. 1):

- National Park *Acacia-Commiphora* – The strongly-protected and highly productive core tourist area of Ruaha National Park, which is dominated by *Acacia-Commiphora* bushland and open grassland habitat. This site 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).

- National Park miombo woodland – The miombo woodland habitat in western Ruaha National Park, which receives less on-the-ground protection than the core tourist area of the National Park due to its remoteness and lower tourist traffic.

- Community-managed area – MBOMIPA WMA, a less-strongly protected area of *Acacia-Commiphora* habitat, which is located in a highly productive area near the Great Ruaha River but is directly adjacent to unprotected village land. This area received a relatively high level of foot patrols in 2018 after several years of absence of law enforcement effort (STEP, 2019).

- Trophy hunting area – The Ikiri hunting block of Rungwa Game Reserve, an area under strong protection where trophy hunting is permitted and was taking place at the time of data collection. The survey site is dominated by miombo woodland.

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.

2.2.2. Survey design

We spaced camera stations according to the smallest hypothesised female home range size, to ensure that all individuals in each survey area had a non-zero probability of capture (Noss et al., 2013; Rovero and Zimmermann, 2016). As we did not have *a priori* information on leopard home range sizes in the study area, we set camera spacing conservatively based on female home range data from similar ecosystems elsewhere in Africa (e.g. 25 km^2 in nearby Piti GR, Tanzania; Caso, 2002). At the same time, we sought to ensure the total area covered by each survey grid exceeded hypothesised average male home range (e.g. 136 km^2 in Piti GR; Caso, 2002), as recommended for robust density estimation (Noss et al., 2013; Tobler and Powell, 2013). Average spacing between stations varied between sites due to logistical factors.

We set stations along roads whenever possible, prioritising junctions, to maximise captures of large carnivores, and added off-road stations 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 and 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 National Park *Acacia-Commiphora* habitat, for 83 days between June and September 2018.

Twenty-six stations (all paired; 52 cameras) were deployed in the National Park miombo woodland, over 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 the community-managed area, 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 trophy hunting area, for 90 days between July and October 2019.

Detailed summary information for the four survey grids can be found in Appendix A.

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 and 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 (see Appendix B), and the trap layout, containing information on the location and activity of each camera station (see Appendix C). Sampling occasions were defined as a 24 hour period from midday to midday, as recommended for nocturnal species (Rovero and Zimmermann, 2016). See Appendix D 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 and 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 Appendix E). 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 (ΔAICc < 2; Burnham and Anderson, 2004), model averaging was used 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.

2.6. Prey relative abundance

We calculated the relative abundance index (RAI) of leopard prey species from the camera trap data from each survey, to provide a measure of prey availability in each study site. We classified 13 mammal species as prey based on known dietary preferences of leopard (Hayward et al., 2006; full details can be found in Appendix F). We calculated RAI for each species by multiplying the number of capture events for that species in each grid by 100, and dividing this by the number of trap nights for that grid (Rovero and 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. We then summed the RAI of each prey species for each survey, to produce a measure of overall prey relative abundance across the different study sites. As we were unable to directly test the effect of prey RAI on leopard density (as this would require RAI values to be extrapolated beyond our station locations; Efford, 2020), we carried out a correlation test between the leopard density estimates and prey RAI for each survey site.

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 Appendix A). Counting only the flank with the greatest number of captures for each survey 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 National Park *Acacia-Commiphora* survey, versus 66.7% in the National Park miombo woodland survey, 50.0% in the community-managed area survey, and 26.3% in the trophy hunting area survey.

Sex was confidently assigned to 83.8% of individuals identified in the National Park *Acacia-Commiphora* (15 female, 16 male, 6 unknown), 83.3% of individuals in the National Park miombo woodland (7 female, 3 male, 2 unknown), 77.3% of individuals in the community-managed area (8 female, 9 male, 5 unknown), and only 47.4% of individuals in the trophy hunting area (4 female, 5 male, 10 unknown). The lower rates of recapture and sex identification in the trophy hunting area were likely a result of wider spacing between stations in this survey. None of the identified individuals were captured across more than one survey site.

3.2. Population density

We estimated density based on left flank captures for the National Park *Acacia-Commiphora*, community-managed area, and trophy hunting area surveys, and from right flank captures for the National Park miombo woodland survey. Buffer width stabilised at 12 km for the National Park *Acacia-Commiphora* survey, 14 km for the community-managed area survey, 16 km for the trophy hunting area survey, and 30 km for the National Park miombo woodland survey.

The top-ranked model of population density was secr.road.sex.s (g0 varies with station location; σ varies with sex) for the survey in National Park *Acacia-Commiphora*, and secr.sex.s (σ varies with sex) for the survey in National Park miombo woodland, in each case being the only model with substantial support. For the surveys in both the community-managed and trophy hunting area, there were two models of density with substantial support (ΔAICc < 2): secr.road.sex.s and secr.sex.s in the community-managed area, and secr.0 (null model) and secr.sex.s in the trophy hunting area. Results of model ranking for all sites can be found in Appendix E. Sex therefore had a significant impact on leopard movement across all four sites, with males moving greater distances than females, while capture probabilities were higher at stations on roads than those on trails in the two *Acacia-Commiphora* sites.

We estimated the highest population density in the National Park *Acacia-Commiphora* site, 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 in the community-managed area, followed by 3.36 ± 1.09 per 100 km^2 in the trophy hunting area, and 3.23 ± 1.25 per 100 km^2 in the National Park miombo woodland site (Table 1; Fig. 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 National Park *Acacia-Commiphora* site (HRCIW = 36.1%) and community-managed area (48.3%) were sufficiently precise to fall below this threshold, but the estimates from miombo woodland in the trophy hunting area (65.6%) and National Park (80.2%) were not (Table 1).

3.3. Prey relative abundance

We estimated an overall prey RAI of 104.8 in the National Park *Acacia-Commiphora*, 73.7 in the community-managed area, 43.5 in the trophy hunting area, and 41.2 in the National Park miombo woodland (Table 1). RAI and capture information for individual prey species can be found in Appendix F. A Pearson's product-moment correlation test between the leopard density estimates and prey RAI showed that these values are highly positively correlated across our four sites ($r(2) = .97$, $p = .031$). We do, however, acknowledge the limitations of this test, as it is based on a very small number of data points, and does not incorporate information on the error in our density estimates.

4. Discussion

This study provides evidence of a globally-important leopard population in the Ruaha-Rungwa landscape of southern Tanzania. In line with our expectations, we estimated a high population density for leopard in the core tourist area of Ruaha National Park, a slightly lower density in the neighbouring community-managed area (MBOMIPA WMA), and the lowest densities in miombo woodlands in a trophy hunting area (Rungwa Game Reserve) and the National Park. These are some of the first such estimates for Tanzania (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 and a community-managed area in the country. We also provide some of the first insights into leopard ecology in a miombo woodland habitat (but see Davis et al., 2020; Jorge, 2012), which represent an important component of the species' range in Africa (~18% of extant range; Olson et al., 2001; Stein et al., 2016).

The density estimates for the core tourist area of Ruaha National Park and the community-managed area are sufficiently precise to detect a critical population decline per IUCN guidelines, suggesting that future surveys at the same sites could provide valuable information on population dynamics via open capture-recapture analysis (Karanth et al., 2006). In contrast, neither density estimate from the miombo woodland sites met this threshold, indicating that caution should be exercised when using these estimates as a baseline for population monitoring. Nevertheless, future surveys in these sites could provide valuable information on mortality through comparisons of photographed individuals.

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 100km^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 100km^2; Havmøller et al., 2019), while our estimate for the core tourist area of Ruaha National Park is higher than the dry season leopard density estimated in the similarly highly-protected Serengeti National Park (5.41 per 100km^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 100km^2; Jorge, 2012), and are higher than the mean density estimated in the human-impacted Central Zambezian miombo woodland of Kasungu National Park, Malawi (1.9 per 100 km^2; Davis et al., 2020).

4.1. Possible drivers of variation in density

Although it was not possible to formally test for the effect of prey on leopard density, the strong correlation between prey availability and leopard density estimates across our four study sites suggests that prey may be a key driver of variation in leopard density within the study landscape. This aligns with studies elsewhere in Africa that have found prey abundance to be an important predictor of leopard population density (Marker and Dickman, 2005; Stein et al., 2011; Boast and Houser, 2012; Rosenblatt et al., 2016).

The high population density estimated in the *Acacia-Commiphora* core tourist area of Ruaha National Park, which also had the highest leopard prey RAI of our study sites, is likely to be a result of this area's strong protection and location near the highly-productive Great Ruaha River, which supports the highest dry season ungulate biomass across the landscape (TAWIRI, 2019).

Despite having similar highly-productive habitat to the core tourist area of the National Park, we found the community-managed MBOMIPA WMA to support a lower density of leopard in the area surveyed. This may be linked to the lower abundance of prey in this site, as indicated by our RAI estimates. The lower availability of prey in this area may itself be a result of edge effects acting on prey populations (Balme et al., 2010): habitat is highly degraded in unprotected lands beyond the WMA's south-eastern boundary (Abade et al., 2018), and prey species in this area are likely to face higher levels of anthropogenic impact than those in our other study sites. Evidence for this is provided by the fact that nine illegal incursions (two picturing captured bushmeat) were photographed in the community-managed area during the survey period, versus two in the trophy hunting area, one in the miombo of the National Park, and none in the core tourist area of the National Park.

In addition to potential edge effects impacting prey populations, there may also be edge effects acting directly on leopard in this area. Bushmeat poaching has been shown to directly contribute to leopard mortality when individuals get caught in snares (Swanepoel et al., 2015), including in the study landscape (Ruaha Carnivore Project, unpublished data), and high levels of human-leopard conflict and anthropogenic mortality are reported in the area (Abade et al., 2018; Dickman et al., 2014).

While we were unable to disentangle the relative importance of bottom-up (prey availability) and top-down (anthropogenic mortality) processes in shaping leopard density in this study, future surveys of the same sites would help answer this question by allowing density and survival rates to be compared between the community-managed area and the core area of the National Park (per Balme et al., 2010; Rosenblatt et al., 2016). Regardless of the exact mechanism by which human encroachment around the community-managed area impacts density, our results are consistent with other studies across Africa which have found negative relationships between leopard population density and human encroachment around PAs (Balme et al., 2010; Havmøller et al., 2019; Henschel et al., 2011; Marker and Dickman, 2005; Rosenblatt et al., 2016).

Whereas the lower recapture rate in the trophy hunting area was likely a result of the wider spacing between stations in this grid, the lower recapture rate in the community-managed area – where stations were spaced more comparably to the grid in the National Park's *Acacia-Commiphora* habitat – could result from the area supporting a greater proportion of transient individuals, such as dispersing sub-adults, than the core area of the National Park (Braczkowski et al., 2015a). If mortality risk is heightened in the area as a result of edge effects, this could indicate that the community-managed area is acting as a population sink.

The lower leopard population density estimated in both miombo woodland sites is probably 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 supported by our prey RAI estimates – which were very similar across the two miombo sites, and lower than those in *Acacia-Commiphora* habitat – and mirrors findings from miombo woodlands in northern Mozambique (Jorge, 2012). 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 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 assigned to different PA types, largely derived from unpublished camera trap studies (MNRT, 2018). The figures currently employed for National Parks (7.9 per 100 km^2) and Game Reserves (4.5 per 100 km^2) are higher than our estimated population densities for Ruaha National Park and Rungwa Game Reserve, respectively, which are each the second largest PA of their type in Tanzania. Although the average estimate used for WMAs (2.3 per 100 km^2) is lower than our estimate for MBOMIPA WMA, this figure also applies to lesser-protected areas where human settlement and livestock grazing are unrestricted, and leopard densities are therefore likely to be lower. Our density estimate from the community-managed area 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 there is evidence of some large carnivore populations existing below carrying capacity in trophy hunting areas (Balme et al., 2010, 2009; Loveridge et al., 2016a; Packer et al., 2010), our results suggest that the studied trophy hunting area supports a leopard population comparable to that in similar habitat in an adjacent photographic tourism area. This is likely a result of the substantial management investment received in the Ikiri block of Rungwa Game Reserve 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 and those that border unprotected village land.

4.3. Insights into the conservation effectiveness of community-management

We provide evidence that the community-managed MBOMIPA WMA is an important area of habitat for leopard and their prey in the Ruaha-Rungwa landscape, by acting as a buffer zone between the National Park and 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 community-managed area is particularly important for wildlife as it lies along the Great Ruaha River, thus protecting one of the few sources of dry season surface water in the landscape. However, as a result of the edge effects that are likely to affect this area, it 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 et al., 2016b). Nevertheless, our results suggest that community-managed areas have the potential to effectively conserve large carnivore populations at relatively high densities, and can play an important role in protecting core populations.

Like MBOMIPA, many community-managed areas elsewhere in Tanzania and across Africa more widely are positioned along the boundaries of strongly-protected areas (WWF, 2014). As such, these areas not only often 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 potential wildlife corridors (Riggio and Caro, 2017), which are particularly important for securing functional connectivity for leopard and other large carnivores (Fattebert et al., 2015). However, despite their potential to contribute to conservation goals, community-managed areas in Tanzania appear to have achieved mixed success in engagement of local communities (Walsh, 2000) and poverty reduction (Keane et al., 2020). Challenges of this kind – which are also faced by similar initiatives elsewhere on the continent – may limit the efficacy of community management as a long-term conservation tool if left unaddressed.

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 and 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 recommend that future studies of leopard prioritise assessments not just in key components of a landscape but also within more marginal zones, to provide a more complete view of species status; in Ruaha-Rungwa, this could be achieved through complementary surveys in vacant or less-protected hunting blocks, less productive areas, and completely unprotected land.

Given the potential 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 aimed at reducing bushmeat poaching and other human impacts in areas adjacent to unprotected land should not only benefit prey populations, but may also help mitigate direct threats to leopard occupying these areas.

We recommend that our results be employed to inform sustainable use management in the Ikiri block of Rungwa Game Reserve. We also encourage the research and hunting communities to collaborate on similar monitoring efforts for hunting areas elsewhere in Africa, to equip policymakers with the information required to set sustainable levels of offtake. If carried out sustainably, trophy hunting has the potential to foster conservation of wildlife with a relatively low ecological footprint (Di Minin et al., 2016; Dickman et al., 2019; Lindsey et al., 2007). We therefore 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., 2015b). Given that trophy hunting areas comprise a significant portion of leopard range in Tanzania (MNRT, 2018) and a number of other African range states (Stein et al., 2016), and law enforcement in many hunting areas is funded primarily through hunting revenues (MNRT, 2018), proposals to phase out trophy hunting must be supported with viable alternative financing or forms of land use, so as not to risk undermining resources for the protection of vital habitat for the species (Di Minin et al., 2016; Dickman et al., 2019).

Finally, given the potentially important role of many community-managed areas in maintaining healthy and connected ecosystems across Africa, as well as their potential contributions to local development, we suggest that support for these areas be considered an international conservation priority. We also recommend the implementation of long-term wildlife monitoring in community-managed areas which are adjacent to highly-protected areas, to assess trends in wildlife populations and monitor edge effects.

Supplementary Material

Summary information for each of the survey grids (Appendix A), capture histories (Appendix B), trap layouts (Appendix C), additional details on the SECR modelling process (Appendix D), results of model ranking (Appendix E), and detailed preferred prey relative abundance indices (RAI; Appendix F) are available in the Supplementary Material.

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Figures & Tables

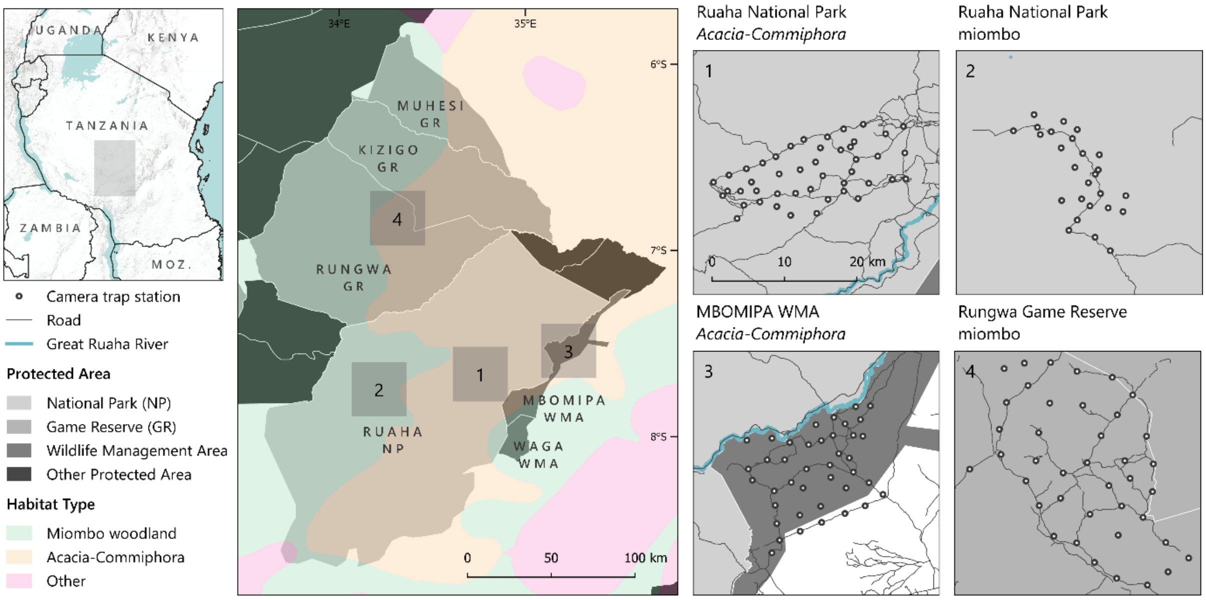

Figure 1: Top left: Location of the Ruaha-Rungwa landscape within Tanzania. Centre: the different land use types in place in the study landscape and the location of camera trap survey areas. Right: detail of camera trap grids in (1) National Park *Acacia-Commiphora* habitat (Ruaha National Park), (2) National Park miombo woodland habitat (Ruaha National Park), (3) a community-managed area (MBOMIPA WMA; *Acacia-Commiphora* habitat), and (4) a trophy hunting area (Rungwa Game Reserve; miombo woodland habitat). Hunting is permitted in Game Reserves and Wildlife Management Areas, but was only carried out in Game Reserves at the time of the study. Note that the survey site in Rungwa Game Reserve is dominated by miombo woodland, but lies at the transition zone with *Acacia-Commiphora* habitat; this is not accurately reflected in the figure due to minor discrepancies in the habitats shapefile.

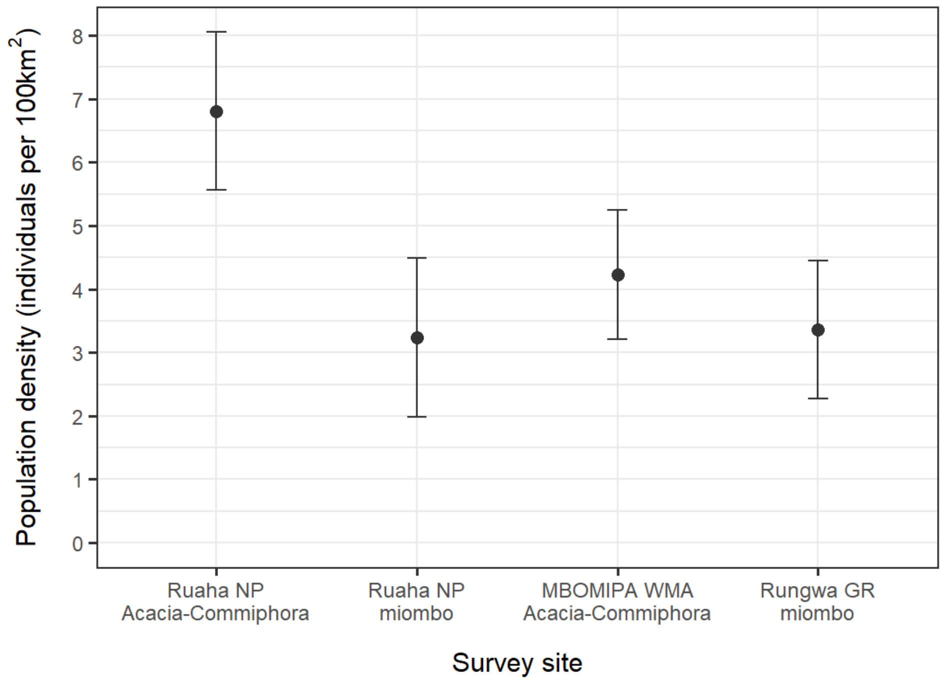

Figure 2: Population density estimates for the four survey sites, with error bars showing the standard error (SE) for each estimate. The trophy hunting area is located in Rungwa Game Reserve, and the community-managed area is in MBOMIPA WMA. Although hunting is permitted in both these sites, it was only carried out in Rungwa Game Reserve at the time of study.

Table 1: Population density and parameter estimates for the four survey sites. Estimates are 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. Additional details are provided on PA name and designation, whether trophy hunting is permitted and was carried out at the time of study, and prey relative abundance in each site.

Parameter	Estimate	**National Park**[1] *Acacia-Commiphora*	**National Park**[2] miombo woodland	**Community-managed area**[3] *Acacia-Commiphora*	**Trophy hunting area**[4] miombo woodland
	PA name	Ruaha	Ruaha	MBOMIPA	Rungwa
	PA designation	National Park	National Park	WMA	Game Reserve
	Trophy hunting permitted	No	No	Yes	Yes
	Trophy hunting carried out at time of study	No	No	No	Yes
	Prey Relative Abundance Index (RAI)	104.8	41.2	73.7	43.5
g0[5]	Mean ± SE		0.015 ± 0.006		0.007 ± 0.003
	95% CI		0.007 – 0.033		0.003 – 0.015
$g0_{on-road}$[5]	Mean ± SE	0.035 ± 0.004		0.022 ± 0.004	
	95% CI	0.028 – 0.044		0.015 – 0.032	
$g0_{off-road}$[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