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Anthropogenic pressure limits the recovery of a postwar leopard population in central Mozambique

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Abstract

The population size and conservation status of wildlife in post-conflict areas is often uncertain. In Mozambique, decades of armed conflict resulted in large-scale wildlife population depletion with limited conservation and research opportunities. The African leopard (*Panthera pardus*) is a large carnivore with great ecological and economic significance, yet their population status is largely unknown within Mozambique. Using camera trapping in conjunction with robust spatially explicit capture-recapture modeling, we estimated leopard density in 2021 for Coutada 11, a wildlife management area in the postwar Zambezi Delta landscape of central Mozambique. Leopard density was relatively low (1.57 ± 0.37 SE [latent-mixture-model] and 1.84 ± 0.41 [sex-mixture-model] leopards/100 km^2), occurring in the bottom fourth of 161 range-wide leopard densities, and similar to those from semiarid and human-dominated landscapes. Prey-based carrying capacity estimates suggested that leopard density should be at least twice as large. Despite a recent and substantial reduction in poaching activity, evidence of snared leopards indicates that sustained bushmeat poaching, combined with sustainable, but additional legal offtake is suppressing leopard population recovery. This study provides important baseline insight into leopard population density in Mozambique and joins mounting evidence indicating that anthropogenic pressures limit large carnivore populations which is of major national and global concern. We suggest long-term monitoring of this leopard population to determine trends over time and implement effective conservation interventions in response to population changes. This population clearly has the capacity to recover if hunting quotas are reduced to account for illegal offtake and, more importantly, if anti-poaching efforts are redoubled to reduce unsustainable anthropogenic mortality of leopards.

KEYWORDS
armed conflict, baseline estimate, camera trapping, hunting quota, low density, Mozambique, *Panthera pardus*, spatially explicit capture-recapture

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1 | INTRODUCTION

Among the most significant threats facing biodiversity are armed conflict and unsustainable anthropogenic mortality. Armed conflict and political instability may drive local population decline and extirpation of wildlife beyond the effective periods and areas of active conflict (Bauer et al., 2022; Loucks et al., 2009; Machlis & Hanson, 2008), although few studies have investigated its ecological impact (e.g., Braga-Pereira et al., 2020; Hanson et al., 2009). Since the 1950s, armed conflicts have occurred in over 80% of the world's biodiversity hotspots (Hanson et al., 2009) and 70% of African protected areas (PAs), which may imperil wildlife populations (Daskin & Pringle, 2018). Counterintuitively, although conflict zones may act as wildlife population sinks, they may also relieve pressure from natural resource utilization through "war/buffer-zone" refugia (Martin & Szuter, 1999), where conflict zones often become depopulated due to the high risk to human life (Hanson, 2018; Hatton et al., 2001). Assuming environmental legislation has been established post-conflict, enforcing such conservation policy is rarely an immediate priority (Daskin & Pringle, 2018). As displaced people resettle near conservation areas and these become safer to use, natural resources in these "communal" landscapes are often exploited either out of necessity or for commercial gain (e.g., informal infrastructural development, subsistence hunting, illegal lumber/charcoal/wildlife trade and professional hunting operations; Hatton et al., 2001; Soto, 2009). However, rapid and sustained conservation intervention post-ceasefire may facilitate habitat and wildlife population recovery (Daskin & Pringle, 2018). For example, large-scale ecosystem restoration following civil unrest facilitated the recovery of ungulate and carnivore populations in Gorongosa National Park, Mozambique (Bouley et al., 2018; Stalmans et al., 2019).

Large carnivores shape ecosystems and flagship conservation efforts (Dalerum et al., 2008; Estes et al., 2011). However, their slow generational turnover and low population density, as well as high energetic and spatial requirements increase their vulnerability to extinction (Ordiz et al., 2013; Ripple et al., 2014). The global decline of large carnivores is often precipitated by several concurrent anthropogenic threats and cascades through trophic levels to the detriment of entire ecosystems (Atkins et al., 2019; Beschta & Ripple, 2009; Estes et al., 2011; Ordiz et al., 2013; Ripple et al., 2014). For instance, the leopard (*Panthera pardus*) is an elusive large carnivore occupying a broad range of habitat types across much of Africa and Asia (Jacobson et al., 2016; Nowell & Jackson, 1996). Despite their apparent adaptability, leopards are considered "Vulnerable" (IUCN Red List, Stein

et al., 2020) having suffered significant population reductions and eradication from vast tracts of their historic distribution, with estimated range declines of 48–67% across the African continent in the past century (Jacobson et al., 2016). Recent evidence suggests that even formal PAs, constituting 17% of remaining leopard range, are not exempt from these anthropogenic threats (Jacobson et al., 2016; Loveridge et al., 2022; Naude, Balme, O'Riain, et al., 2020; Rogan et al., 2022). Leopards are predicted to experience further population declines across sub-Saharan Africa over the next 50 years due to loss of habitat and prey populations (Stein et al., 2020; Wolf & Ripple, 2016). Reliable assessments of leopard distribution, population density and status are thus key to their effective conservation (Jacobson et al., 2016; Karanth & Nichols, 2002; Stein et al., 2020).

Remote sensing technology has become a common tool for studying cryptic and wide-ranging species (Balme, Hunter, & Slotow, 2009). Camera trapping in particular, provides a non-invasive and increasingly cost-effective means of monitoring carnivore populations (O'Connell et al., 2011). Various analytical techniques such as spatially explicit capture-recapture (SECR) models have been developed to estimate population densities of individually identifiable carnivore species (i.e., through unique pelage or vibrissae patterning) from camera-trap imagery (Borchers & Efford, 2008; Gopalaswamy et al., 2012). Unlike classical capture-recapture (CR) methods, SECR models incorporate spatial information of each individual's detection history and a defined state-space in the density estimation process (Efford & Fewster, 2013; Royle et al., 2014). Therefore, SECR analysis estimates density explicitly, as opposed to subjectively through ad hoc calculations in CR analysis. Obtaining accurate and precise density estimates of understudied carnivore populations are crucial for improving our understanding of the factors influencing these populations and our ability to better conserve these species.

In Mozambique, leopards were once abundant and widespread (Smithers & Tello, 1976). However, during and after decades of armed conflict, particularly the Mozambican Civil War (1977–1992), wildlife populations were decimated (Beilfuss et al., 2010; Hatton et al., 2001; Soto, 2009; Stalmans et al., 2019). Although there are no accurate records of the impact on leopard populations (Purchase & Mateke, 2008), given that leopard densities are often positively correlated with prey biomass (Marker & Dickman, 2005), it is assumed that leopard populations suffered concurrent declines during this period (Chardonnet et al., 2009). For example, leopards, spotted hyenas (*Crocuta crocuta*) and African wild dogs (*Lycaon pictus*) were extirpated from the flagship conservation area, Gorongosa

National Park (Pringle, 2017), while cheetahs (*Acinonyx jubatus*) were considered extirpated throughout Mozambique (Soto, 2009, but see Andresen et al., 2012). The immediate postwar period was overshadowed by uncontrolled exploitation of wildlife and other natural resources through ineffective law enforcement, which was especially intense where high densities of displaced people bordered conservation areas (Hatton et al., 2001). Warfare ceased in 1992 and enforcement has since improved; however, bushmeat poaching (i.e., for subsistence and commercial trade) has continued as a proximate threat (i.e., either targeted or as bycatch), placing further pressure on remaining carnivore and prey populations. Increasing evidence suggests that leopards and other large carnivores may also be targeted by this unsustainable form of offtake to supply the illegal wildlife trade (Everatt et al., 2019; Lindsey et al., 2013). In contrast, leopards are legally hunted in a number of wildlife management areas (WMAs, i.e., a landscape set aside for use and management of wildlife) across Mozambique (MITADER, 2018; Strampelli et al., 2018), representing an important species for the country's regulated trophy hunting industry (Jorge et al., 2013; Lindsey et al., 2012). While sustainable trophy hunting can fund essential anti-poaching efforts and foster conservation (Lindsey et al., 2007), offtake quotas need to account for the additional pressures of bushmeat poaching (i.e., through wire-snaring and gin-trapping, hereafter "snaring") in the landscape and should be based on reliable density estimates to prevent leopard population declines (Packer et al., 2011).

This study aims to use remote camera trapping and SECR-based approaches to determine the baseline population density of a postwar recovering leopard population within the large, unfenced Zambezi Delta (hereafter, the Delta) landscape of central Mozambique. This leopard density is then contextualized relative to studies of comparable habitat suitability and management regime, as well as local prey availability, trophy hunting and bushmeat poaching via a stepwise exclusionary approach. These findings are discussed in the context of regional carnivore population recovery and management.

2 | METHODS

2.1 | Study area

We surveyed leopards within the Coutada 11 (1930 km²) WMA in central Mozambique. Coutada 11 forms part of the Marromeu-Coutada Complex (9754 km²), which falls within the southern half of the Delta, and was declared a RAMSAR wetland site of international importance in 2003 (Beilfuss et al., 2010). This landscape is administratively divided into the Marromeu National Reserve, and four WMAs, including Coutada 11 (Figure 1). The climate is classified as tropical with hot-wet summers (November–April) and cool-dry winters (May–October), and a mean annual rainfall of 1000–1400 mm (Beilfuss et al., 2000). The landscape is very flat and poorly drained (Bento et al., 2007). The delta supports a variety of habitat types ranging from slightly higher-lying sand forest and Miombo woodland with interspersed shallow wetland pans in the west, to lower-lying floodplain grassland and papyrus swamp in the east (Beilfuss et al., 2000). The landscape supports a variety of forest- and floodplain-dwelling ungulates and large carnivore species including resident leopard, spotted hyena, as well as reintroduced lion (*Panthera leo*) and cheetah (Briers-Louw et al., 2023). Historically, this delta ecosystem supported large concentrations of wildlife, including herds of African buffalo (*Syncerus caffer*) and waterbuck (*Kobus ellipsiprymnus*) both peaking at around 45,000 individuals (Hatton et al., 2001). However, the Delta has undergone centuries of utilization, with records extending back to the 12–14th centuries (Tinley, 1977), while Maugham (1914) described local people using "log-built traps" to kill leopards for traditional use. Later, decades of armed conflict and unsustainable culling operations resulted in large-scale wildlife population depletions, with some being reduced to 5% of their historical numbers (Beilfuss et al., 2010; Hatton et al., 2001). Hunting recommenced following cessation of the warfare in 1992. With an influx of foreign clientele, and subsequent funding and enforcement by localized anti-poaching units to control bushmeat poaching, wildlife populations started to recover naturally (Beilfuss et al., 2010). While bushmeat poaching remains prevalent and requires active anti-poaching intervention, ungulate populations continue to increase, with over 80,000 animals estimated in the landscape in 2021 (Macandza et al., 2022), while relatively little is known about the large carnivore populations.

2.2 | Camera trapping

Two pilot camera trapping surveys were conducted in Coutada 11 in 2019 and 2020, followed by a comprehensive survey in 2021 (Figure 1). The 2019 survey used a fine-scale 2 × 2 km grid sampled for 60 days, which was expanded to a 4 × 4 km grid sampled for 64 days in 2020 to improve area coverage, while attempting to optimize leopard recaptures. The comprehensive 2021 survey used the same 4 × 4 km grid, although more camera traps were available to improve coverage and fill in potential "gaps" in the survey design. Each survey area was divided into two adjacent grids and sampled sequentially for
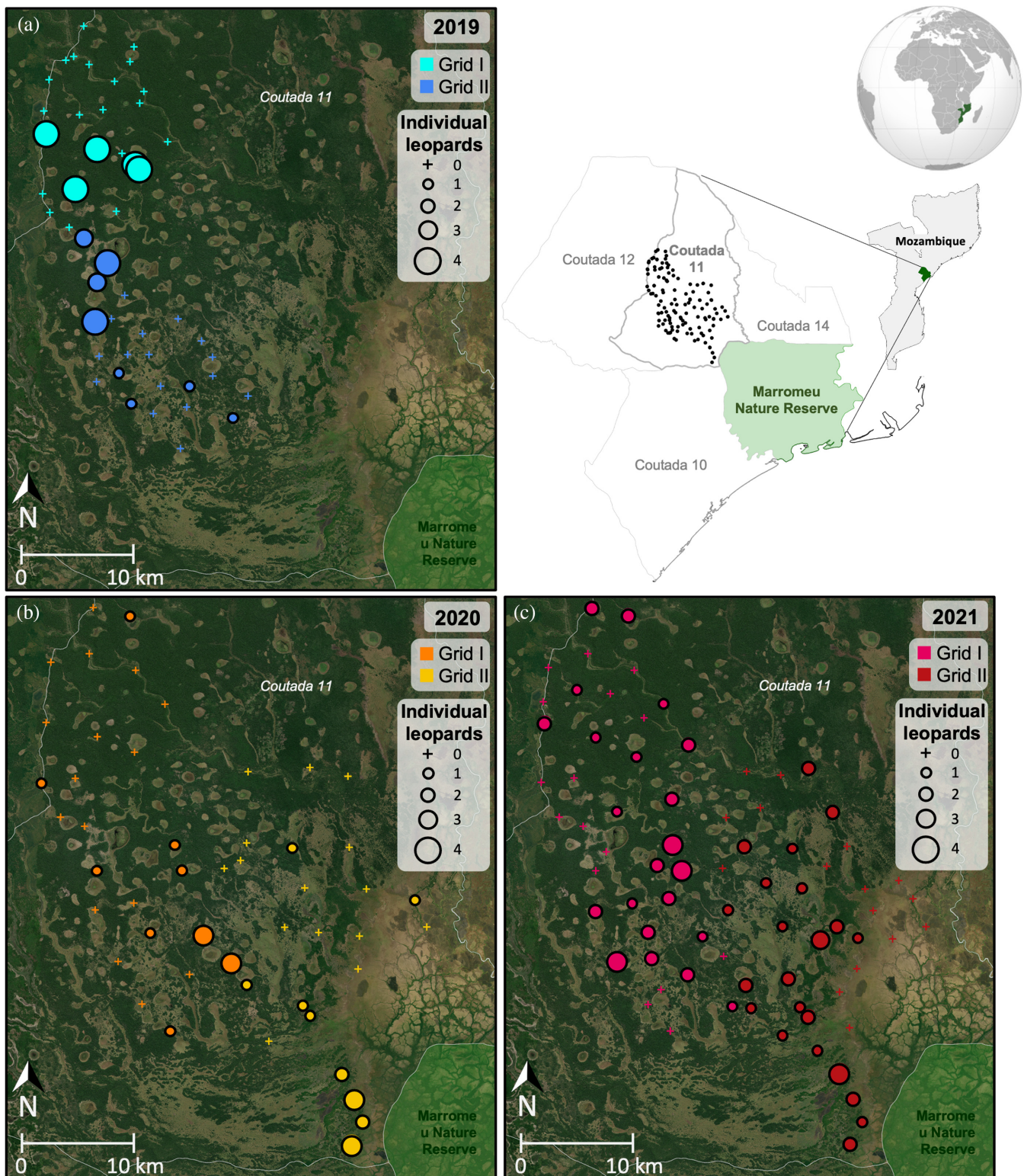
FIGURE 1 Coutada 11 study area in the Zambezi Delta of Mozambique, detailing the sampling design for baseline leopard density estimates in 2019 (A; grid 1 = light blue; grid 2 = blue), 2020 (B; grid 1 = yellow; grid 2 = orange), and 2021 (C; grid 1 = pink; grid 2 = red), using a multi-(2019–2021) and single-session (2021) spatially explicit capture–recapture (SECR) framework.

improved sample area coverage (Karanth & Nichols, 2002). The study area coverage met SECR assumptions, in that it was sufficiently expansive to

encompass a large leopard home range and sufficiently intensive to ensure multiple spatial recaptures of individuals. Inter-trap distance was determined by a regional

estimate of minimum female home range size (14 km^2; Balme, Hunter, & Slotow, 2009), resulting in at least two camera trap stations within the home range of every individual. The 140-day sampling period may have led to violation of the assumption of population closure ($Z = -5.59$, $p < .001$), but we opted to follow the recommendations of Dupont et al. (2019) to extend the sampling period on the basis that for such a sparse, data-scarce population of a species with a moderately slow life history and unsynchronized breeding, the longer survey period constituted a worthwhile trade-off between slight bias for much greater precision. Camera trap stations were placed along roads and trails of known or suspected leopard movement, comprising two opposing traps ~2 m from the path, mounted on wooden poles or trees at ~50 cm above the ground. Unique, asymmetrical pelage patterning in leopards is captured by paired trapping for simultaneous left and right lateral body images which facilitate individual identification (Müller et al., 2022). Standard camera trap settings and field techniques were applied in all surveys (Palencia et al., 2022).

2.3 | Data processing

Camera trap images were classified to the species level and processed using the *camtrapR* (Niedballa et al., 2016) package in R v. 4.2.0 (R Core Team, 2022). *Hotspotter* (Crall et al., 2013) pattern recognition software was then used to identify individual leopards (Nipko et al., 2020), which was verified through consensus among five independent researchers. Sex was determined through the presence of external genitalia, dew lap size, frontal bossing and considerations of overall body shape and size (Balme et al., 2012), although sex was classified as unknown when consensus could not be reached. Independent captures were defined using an 8-h interval (Rogan et al., 2022), such that we recorded the total number of independent captures of each individual at each trap over the course of each survey period. Visible signs of poaching pressure (e.g., scars or open wounds around the neck, body or legs sustained while trying to escape a wire-snare or gin trap) were also recorded (Loveridge et al., 2020).

2.4 | Density estimation

Leopard density was estimated using a closed population SECR framework with inhomogeneous density in the package *secr* (Efford, 2022). SECR is a form of hierarchical model with a state process representing density and an observation process representing the expected probability or rate of captures based on the assumption that

probability of detection decreases as the distance between a detector and an animal's activity center increases. In this study, Poisson processes were assumed for both these states. Density was expressed as a point process representing the intensity of activity centers within the state space. In accordance with our definition of independent captures and for computational efficiency, we modeled observations using a "count" detector formulation. The expected number of observations of individual i at trap j was assumed to vary as a function of the distance between trap j and the activity center of individual i following a hazard half-normal function with two parameters: baseline detection rate (λ_0) and spatial decay parameter (σ; Efford et al., 2009; Royle & Gardner, 2011). All models were fitted by maximizing the full likelihood (Borchers & Efford, 2008) using the Nelder–Mead optimizer.

To ensure models converged correctly, we used parameter estimates from a model with homogeneous density as starting values for more complex models with inhomogeneous density. We tested a range of buffer widths around the trap array to define the modeling state space and selected the minimum threshold at which density estimates stabilized in a naïve model (i.e., no covariates for any parameters). All SECR input files and R code can be accessed in Appendix S1.

SECR density estimates are generally robust to misspecification of the detection model (Dey et al., 2022). However, they are prone to bias when heterogeneity in detection within the population is unmodeled (Gerber & Parmenter, 2015). We tested various trap-level and individual-level effects on the detection process to account for potential sources of bias. We fit two sets of detection models to account for different hypotheses regarding potential sources of heterogeneity within the population. The first set hypothesized that detection-model parameters (i.e., λ_0 and σ) varied according to sex, which we incorporated into the model using a two-class partially observed hybrid mixture since not all individuals could be sexed with certainty. The second set of models was formulated to control for the possibility of some otherwise unknown source of behavioral heterogeneity affecting detectability within the population, for example due to breeding or dispersal. We controlled for such unmodeled sources of heterogeneity in the second set of models using a two-class latent mixture. For both sets of models, the mixture classes were included as covariates for both λ_0 and σ.

2.5 | Model selection

The first set of candidate models consisted of single-session SECR models with latent or hybrid mixture

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models on both λ_0 and σ using the 2021 survey. A second set of multi-session candidate models was then fitted using all three surveys (2019–2021) with parameter estimates static across sessions. As with the long survey period, the multi-session models represented a trade-off between bias and precision. The added capture histories from 2019 to 2020 were expected to improve precision while the assumption of static density among sessions and violating the assumption of independent individuals could introduce small amounts of bias, which we considered tolerable. However, these exploratory multi-session models were not included in further analyses as these not only violated certain assumptions by including surveys of smaller sampling effort, but also did not improve the precision as expected (Tables S1 and S2). Models within each candidate set were compared using Akaike's information criterion corrected for small samples sizes (AIC$_c$; Burnham & Anderson, 2002). Top performing models were selected on the parsimony principle, where complex models for which a nested model showed support (i.e., $\Delta AIC_c < 2$) were only considered to be supported if they outperformed the nested model according to a likelihood ratio test. We tested the validity of all the assumptions underpinning the single session model formulation using post hoc goodness-of-fit (GOF) tests to determine whether the parameter estimates were consistent with the data. Specifically, the GOF tests provided a check for potential overdispersion in the Poisson observation process and for poor fit of the mixture models. Model fit was quantified as the ratio of model deviance to the residual degrees of freedom and compared to the deviance of 99 models simulated from the model parameter estimates using Monte Carlo resampling. We considered fit adequate if the model ranked between the 10th and 90th percentiles compared to the simulated models.

2.6 | Factors influencing density

Leopard density was hypothesized to be influenced by the availability of suitable habitat (Searle et al., 2021) and degree of human activity (e.g., Loveridge et al., 2022). We tested these hypotheses by incorporating one or more of these variables as covariates of density ("D") in the SECR models. While leopard density is postulated to correlate with prey abundance (Marker & Dickman, 2005; Rosenblatt et al., 2016; Searle et al., 2021), habitat type was used a proxy for prey availability due to the lack of reliable spatially varying estimates of prey abundance beyond the camera station locations (Efford, 2022). Suitable habitat and human activity were thus tested as mask covariates (Table 1). The European Space Agency Climate Change Initiative (CCI) 20 m resolution land cover

S2 prototype dataset for Africa (ESA [European Space Agency], 2017) was split into four independent categories (i) grassland, (ii) shrubland, (iii) tree cover, and (iv) community/cropland (i.e., defined as non-suitable leopard habitat) using QGIS v. 3.22.8 (QGIS Development Team, 2022). The proportion of each land cover type in a 7 km buffer around each mask point was tested for autocorrelation (Pitman et al., 2017). Proportional coverage of "shrubland" and "community/cropland" were inconsequential and subsequently removed, while proportion of "tree cover" and "grassland" were highly correlated ($r = -.96$), thus "tree cover" was used as a measure of landscape-level habitat. Log-transformed distance to the closest community was included as a proxy for relative human activity. These continuous predictor variables were scaled to a mean of 0 and a standard deviation of 1. Detector covariates of site-level habitat (i.e., tree cover or open vegetation in the area immediately surrounding each detector), human activity index and relative abundance index of preferred prey (Appendix S2) were included as predictors of baseline detection rates (i.e., λ_0), while leopard life history (i.e., classified using a two-class latent mixture or a partially observed two-class sex mixture) was tested as a covariate for baseline detection (λ_0) and spatial decay (σ) of observation rates.

To contextualize this Delta density estimate, an informal review of density literature was conducted in the Web of Science database and search engine Google Scholar, and similar sites were compared across leopard range. Prey abundance data were obtained from three annual (2019–2021) and two biennial surveys (2019 and 2021) in Coutada 11 and the Delta, respectively (Macandza et al., 2022) and formed the basis of two alternative prey-based leopard carrying capacity estimates (Hayward et al., 2007) in these areas, using either preferred prey species or preferred prey weight range. As no dietary studies yet exist for leopards in the Delta, dietary preferences from a nearby PA with similar prey composition were used to derive preferred prey species (i.e., bushbuck, *Tragelaphus scriptus*; common duiker, *Sylvicapra grimmia*; common reedbuck, *Redunca arundinum*; nyala, *Tragelaphus angasii*) and preferred prey weight range (16–47 kg; Briers-Louw & Leslie, 2020). Leopard trophy hunting quota and offtake data for the Delta (2017–2021) were summarized (CITES Trade Database—https://trade.cites.org/). Anti-poaching data were obtained from routine patrols within Coutada 11 (2017–2021) and summarized annually. While anti-poaching patrols are inherently adaptive in nature and thus not standardized (Becker et al., 2013), anti-poaching unit size, enforcement strategies and funding have remained relatively consistent resulting in a stable level of effort over this period.

TABLE 1 Covariates hypothesized to influence leopard detection and density in the Zambezi Delta.

Covariate	Descriptor	Data type	Prediction	Transformation	Covariate type	Reference
Distance to community	Comm_log	Distance of camera traps stations to nearest human settlements	Leopard density is negatively affected by human disturbance	Distance to community calculated in meters and log-transformed. (Scaled to have a mean of 0 and standard deviation of 1)	Density/mask	Balme et al., 2010; Rosenblatt et al., 2016; Havmøller et al., 2019
Habitat (landscape-level)	TreeCover	Proportion of tree cover	Leopard density may be influenced by habitat as habitats vary in productivity	Proportion of tree cover in a 7 km buffer around each mask point (Scaled to have a mean of 0 and standard deviation of 1)	Density/mask	Searle et al., 2021
Human activity index	HumanIndex	Relative abundance index of humans per camera station	Leopard detection is negatively affected by human activity	None	Detector	Rogan et al., 2022
Habitat (site-level)	Habitat	Habitat type (i.e., tree cover or open vegetation) around each camera trap station	Leopard detection may be influenced by the extent of tree cover	Floodplain, shrubland, and pan vegetation classes were pooled as open. Forest, woodland, and riparian vegetation classes were pooled as tree cover.	Detector	Balme et al., 2019
Prey abundance index	PreyIndex	Relative abundance index of preferred prey species	Leopard detection may by positively influenced by the relative abundance of preferred prey	None	Detector	Balme et al., 2019; Ramesh et al., 2017

3 | RESULTS

3.1 | Sampling effort

Overall effort comprised 8152 trap nights over three annual surveys (2019–2021), resulting in 407 leopard images representing 210 independent leopard capture events (Table 2; Figure 2), from which a total of 28 individual leopards were identified (15 females, 10 males, and 3 of unknown sex). The 2019 survey comprised 1423 trap nights across 48 stations resulting in 25 independent leopard captures at 13 stations (naïve occupancy = 27%; spatial recaptures = 12 [spatial recapture rate = 71%]) and yielded a total of seven individuals (females = 5; males = 2). The 2020 survey comprised 1491 trap nights across 48 stations resulting in 37 independent leopard captures at 17 stations (naïve occupancy = 35%; spatial recaptures = 15 [spatial recapture rate = 56%]) and yielded a total of nine individuals (females = 2; males = 6; unknown = 1). The 2021 survey comprised

TABLE 2 Summary of the camera trapping sample effort and leopard capture details across the three surveys (2019–2021) in Coutada 11, Mozambique.

Survey	2019	2020	2021
Survey period	8 Oct–13 Dec	28 Sep–9 Dec	12 Jul–16 Dec
Survey area	269 km^2	641 km^2	619 km^2
Survey duration (nights)	60	64	170
Sampling effort (nights)	1423	1491	5238
Camera stations	48	48	76
Inter station spacing	1.58 km (0.40–3.03 km)	2.75 km (0.99–4.56 km)	2.09 km (0.99–3.60 km)
Independent captures	25	37	148
Percentage of identifiable captures	98%	100%	100%
Individuals recorded	7	9	21
Female	5	2	14
Male	2	6	5
Unknown	0	1	2
Spatial recaptures (SR rate)[a]	12 (71%)	15 (56%)	57 (81%)

[a]Percentage of identified individuals recaptured at more than one station during the survey.

5238 trap nights across 76 stations resulting in 148 independent leopard captures at 45 stations (naïve occupancy = 59%; spatial recaptures = 57 [spatial recapture rate = 81%]) and yielded a total of 21 individuals (females = 14; males = 5; unknown = 2).

3.2 | Density estimation

The highest-ranking (AIC$_c$) single-session (2021) SECR model ($\lambda_0 \sim$ (h2 + Habitat), $\sigma \sim$ h2) showed significantly (ΔAIC$_c$ >2) more support than all alternative models including ecological and anthropogenic determinants of density (Table 3). Estimated leopard density derived from the best-fit single-session models were 1.57 $\pm$ 0.37 [SE] leopards/100 km^2 (CI = 1.00–2.47) and 1.84 $\pm$ 0.41 (CI = 1.19–2.84) using latent- and sex-mixtures, respectively (Table 4). GOF tests did not exclude either of the top single-session models (Table 4).

3.3 | Contextualizing leopard density

Considering all informally reviewed leopard density estimates ($n = 161$) from 76 different studies, the Delta falls within the bottom fourth of range-wide leopard density estimates (Figure 3, Table S3). When classified by comparable management type (Figure 3), leopard density (1.00–2.84 leopards/100 km^2) was most similar to three WMAs in Zimbabwe (1.0–1.7; Loveridge et al., 2022). Estimated prey-based leopard carrying capacities across all aerial

surveys (Coutada 11 and the Delta) were generally consistent across years (2019–2021; Table 5), ranging between 3.0 and 3.5 (preferred prey species) and 8.8–9.3 (preferred prey weight range) and were, on average, double the SECR-based estimates. During the study, four adult male leopards were trophy hunted in Coutada 11 (Table 6). Two leopards in 2019 shortly before the first survey, as well as one leopard (11% of identified individuals) in 2020 and one leopard (5% of identified individuals) in 2021. Anti-poaching patrol data (2017–2021) revealed a steady decrease in poaching and snaring activity over time (Table 7), while photographic evidence found no leopards affected by bushmeat snaring in the 2019 and 2020 surveys, but at least three leopards (11% of identified individuals) were detected with visible signs of snaring injuries in 2021 (Figure 4).

4 | DISCUSSION

Understanding the status and population density of large carnivores is crucial for their conservation, particularly when populations have been exposed to pervasive anthropogenic impacts and contributes directly to the successful recovery and ongoing management of threatened populations (Loveridge et al., 2022). This study used a robust camera trap and SECR approach to provide a baseline density estimate of 1.00–2.84 leopards/100 km^2 for Coutada 11 in central Mozambique. Considering postwar recovery, prey-based carrying capacity (Hayward et al., 2007) of 3.0–9.3 leopards/100 km^2, recent legal
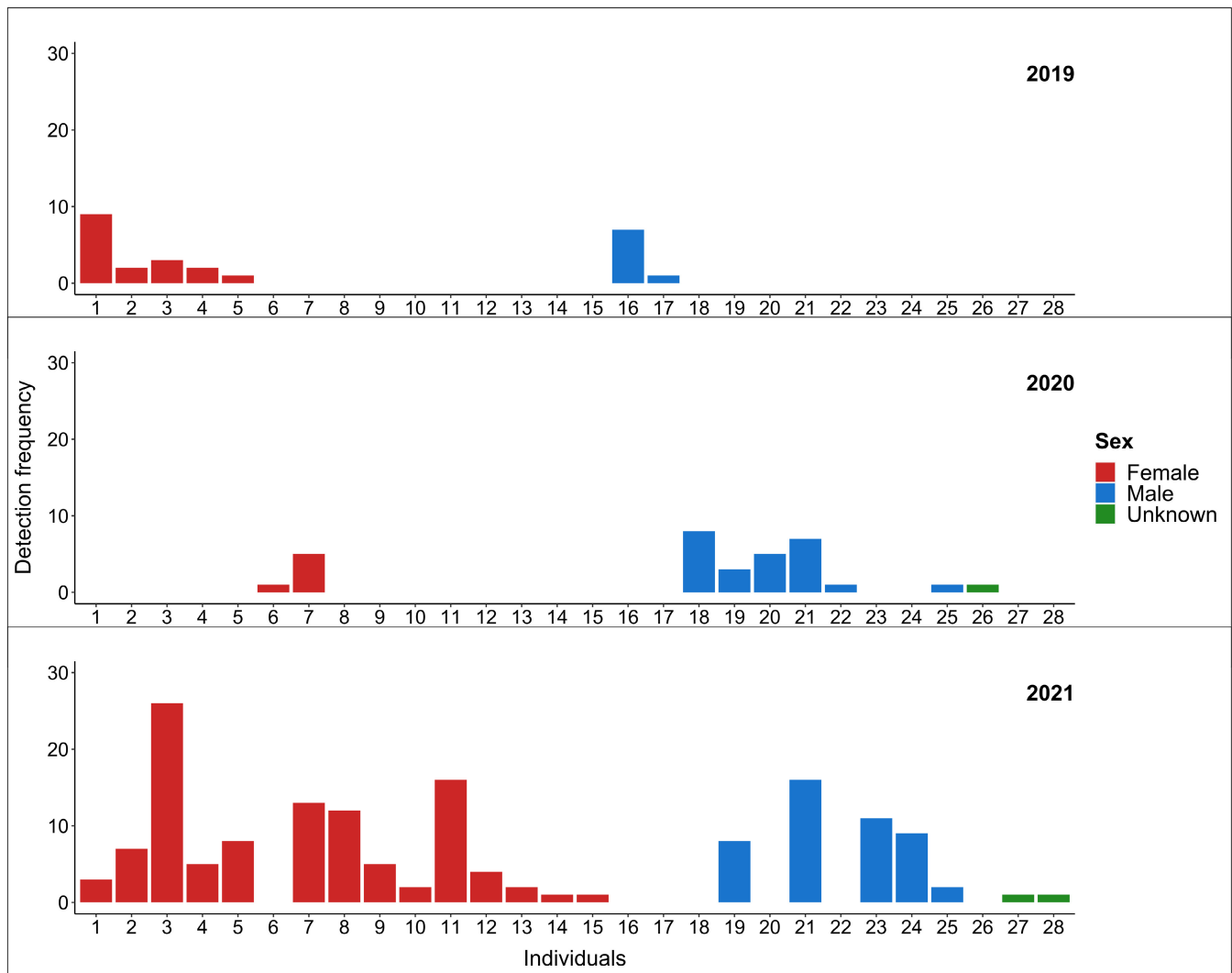
FIGURE 2 Comparison of detection frequency for all demographic classes (females = red, males = blue; unknown sex = green) between 2019, 2020, and 2021 surveys in Coutada 11 in the Zambezi Delta of Mozambique. Each ID code on the x-axis refers to an individual leopard.

offtake being below a potentially sustainable hunting quota (Packer et al., 2011) of 0.1 leopards/100 km², and that poaching pressure in Coutada 11 has decreased substantially in recent years but clearly remains a severe threat, this estimate was substantially lower than expected when compared to similar ecosystems and management regimes.

This leopard density estimate represents one of few from WMAs (i.e., 17 of 161 estimates reviewed), falling among the lower end of densities throughout Africa or Asia and below records in similar mixed forest and seasonal floodplain habitats (e.g., 4.80–8.38, Tembe Elephant Park, South Africa, Ramesh et al., 2017, Rogan et al., 2019; 3.34–7.89, Kafue National Park, Zambia, Vinks et al., 2021). However, this relatively low estimate may be typical of semiarid environments (1.18, Devens et al., 2019; 2.20, Faure et al., 2021; 1.53–1.62, Müller et al., 2022; 1.83, Portas et al., 2022) and human-impacted landscapes (2.49, Balme et al., 2010; 2.7, Henschel et al., 2011; 1.9, Davis et al., 2020; 0.66, Power et al., 2021; 0.7–1.8, Loveridge et al., 2022). Excluding the extirpation and subsequent reintroduction of leopards into nearby Gorongosa National Park (Easter et al., 2019; Gaynor et al., 2021) and the extremely low densities in Coutada 9 (Lindsey & Bento, 2012), this represents the lowest of only four studies (2.60–5.90, Xonghile/Karingani Game Reserve, Strampelli et al., 2018, Niassa Special Reserve, Jorge, 2012) that have estimated leopard density throughout Mozambique. Leopards are severely understudied in central Mozambique and our study represents the first robust density estimate for the region.

Leopard population density may be influenced by various ecological drivers such as habitat or prey availability and competition (Ramesh et al., 2017; Searle et al., 2021).

TABLE 3 Single-session (2021) spatially explicit capture-recapture (SECR) models for leopard density ranked according to Akaike information criterion corrected for sample sizes (AIC_c).

Model	df	AIC_c	ΔAIC_c	Weight
hcov = latent-mixture				
$D \sim 1, \lambda_0 \sim (h2 + Habitat), \sigma \sim h2$	7	591.38	0.00	0.88
$D \sim 1, \lambda_0 \sim (h2 + Habitat+HumanIndex), \sigma \sim h2$	8	596.27	4.89	0.08
$D \sim 1, \lambda_0 \sim h2, \sigma \sim h2$	6	597.36	5.98	0.04
$D \sim Comm\_log, \lambda_0 \sim h2, \sigma \sim h2$	7	601.43	10.05	0.00
$D \sim TreeCover, \lambda_0 \sim h2, \sigma \sim h2$	7	601.56	10.19	0.00
$D \sim 1, \lambda_0 \sim (h2 + PreyIndex), \sigma \sim h2$	7	601.73	10.34	0.00
$D \sim 1, \lambda_0 \sim (h2 + HumanIndex), \sigma \sim h2$	7	601.94	10.56	0.00
$D \sim TreeCover+Comm\_log, \lambda_0 \sim h2, \sigma \sim h2$	8	605.79	14.41	0.00
$D \sim TreeCover*Comm\_log, \lambda_0 \sim h2, \sigma \sim h2$	9	611.90	20.52	0.00
hcov = sex-mixture				
$D \sim 1, \lambda_0 \sim (h2 + Habitat), \sigma \sim h2$	7	621.36	0.00	0.88
$D \sim 1, \lambda_0 \sim (h2 + Habitat + HumanIndex), \sigma \sim h2$	8	626.48	5.12	0.07
$D \sim 1, \lambda_0 \sim h2, \sigma \sim h2$	6	626.81	5.45	0.06
$D \sim TreeCover, \lambda_0 \sim h2, \sigma \sim h2$	7	629.53	8.17	0.00
$D \sim Comm\_log, \lambda_0 \sim h2, \sigma \sim h2$	7	629.75	8.39	0.00
$D \sim 1, \lambda_0 \sim (h2 + PreyIndex), \sigma \sim h2$	7	629.77	8.41	0.00
$D \sim 1, \lambda_0 \sim (h2 + HumanIndex), \sigma \sim h2$	7	629.91	8.55	0.00
$D \sim TreeCover+Comm\_log, \lambda_0 \sim h2, \sigma \sim h2$	8	634.40	13.04	0.00
$D \sim TreeCover*Comm\_log, \lambda_0 \sim h2, \sigma \sim h2$	9	641.48	20.12	0.00

TABLE 4 Specifications of the top ranked single-session (2021) spatially explicit capture-recapture (SECR) models. Density is given in leopards/100 km². N for Coutada 11 calculated at a conservative 1800 km² (excluding non-suitable leopard habitat).

Model parameters	Latent-mixture	Sex-mixture
N_{C11}	28 (18–44)	33 (21–51)
D ± SE	1.57 ± 0.37	1.84 ± 0.41
95% CI	1.00–2.47	1.19–2.84
GOF	0.72	0.86
	h2 = 1	h2 = female
$\lambda 0$ ± SE	0.01 ± 0.00	0.03 ± 0.01
σ ± SE	4405 ± 476	2277 ± 152
pmix	0.52	0.81
	h2 = 2	h2 = male
$\lambda 0$ ± SE	0.04 ± 0.01	0.01 ± 0.00
σ ± SE	2023 ± 155	4337 ± 463
pmix	0.48	0.19

Despite decades of armed conflict, natural habitat within the Delta has remained largely intact, with extensive tree coverage and vast tracts of annual inundation. While the landscape-level habitat covariate did not appear to influence leopard density, site-level habitat affected leopard detectability in the study area (i.e., leopards are more detectable at stations surrounded by tree cover), and likely represents leopard preference for established trails or roads in more densely vegetated areas (Balme et al., 2019; Verschueren et al., 2021). Although prey populations crashed postwar, they rapidly increased following the introduction of sustained anti-poaching efforts. The landscape now supports a relatively high prey biomass of 1485–1538 kg/km² following natural recovery (Beilfuss et al., 2010; Macandza et al., 2022), and yet leopard density is at most half of prey-based carrying capacity (Hayward et al., 2007) for Coutada 11. Competition with other large carnivores may also influence leopard density, especially at high competitor densities (Loveridge et al., 2022; Ramesh et al., 2017); however, competitive exclusion is unlikely as no large carnivores yet occur at medium or high densities in the Delta (Beilfuss et al., 2010).

Anthropogenic pressures are also a strong determinant of leopard density (Loveridge et al., 2022; Rogan et al., 2022; Searle et al., 2021). Studies have revealed that human-dominated peripheries of PAs often negatively
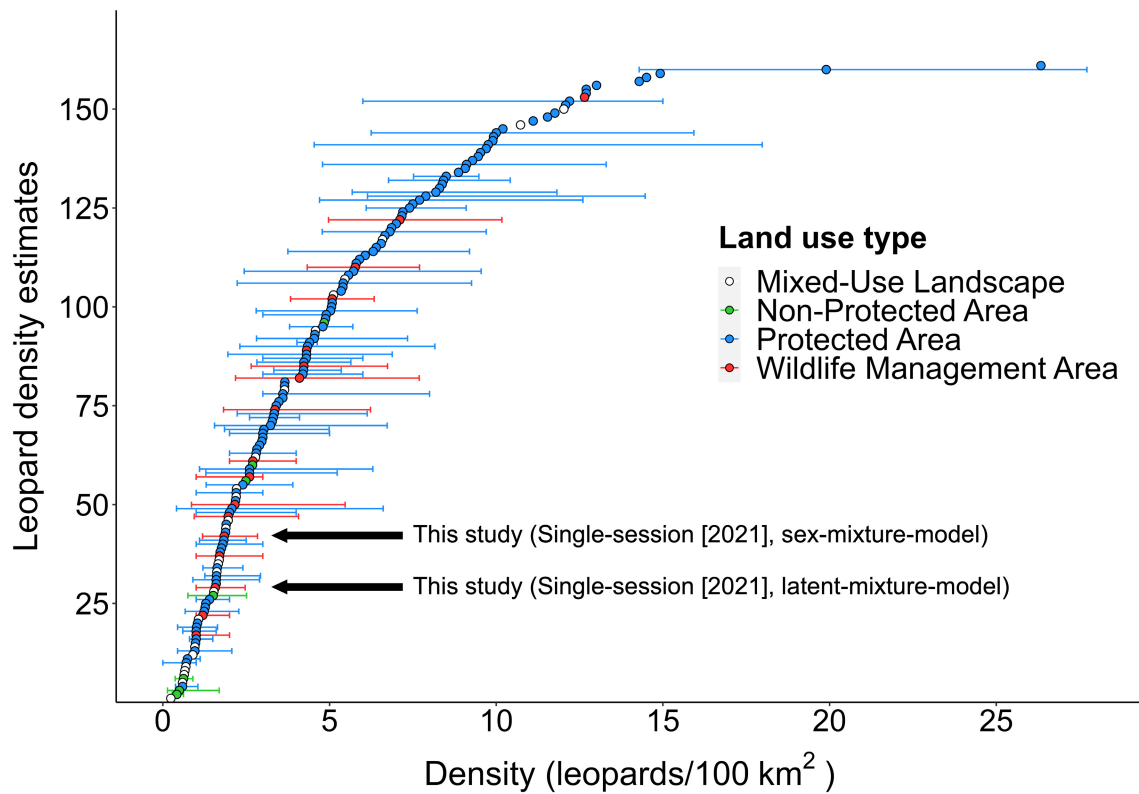
FIGURE 3 Range-wide leopard population density estimates ($n = 161$) derived from camera trapping data and spatially explicit capture-recapture (SECR) or conventional capture-recapture (CR) approaches across studies ($n = 76$). Dots represent mean density estimates and bars represent confidence intervals. Colors of dots and bars indicate land use type and the black arrow indicates density estimates from this study.

TABLE 5 Estimated prey-based leopard carrying capacities for Coutada 11 (2019–2021) and Zambezi Delta (2019 and 2021) based on the Hayward et al. (2007) model. Estimates were generated using preferred prey species and preferred prey weight range derived from Briers-Louw and Leslie (2020).

| Aerial game count | Year | Estimated density (leopards/100 km²) | | Estimated leopard abundance | |
		Preferred prey species	Preferred prey weight range	Preferred prey species	Preferred prey weight range
Zambezi Delta	2019	3.4	9.0	332	876
	2021	3.0	8.8	292	857
Coutada 11	2019	3.5	9.3	68	179
	2020	3.3	9.1	64	175
	2021	3.5	9.2	68	178

TABLE 6 Annual trophy hunting quota and actual offtake (in parentheses) of leopards in the Zambezi Delta between 2017 and 2021. Legal harvest and export of leopards is limited to males (MITADER, 2018).

Location	2017	2018	2019	2020	2021
Coutada 10	2 (2)	2 (2)	2 (2)	2 (2)	2 (2)
Coutada 11	2 (2)	2 (2)	2 (2)	2 (1)	2 (1)
Coutada 12	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Coutada 14	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Marromeu National Reserve	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Total	4 (4)	4 (4)	4 (4)	4 (3)	4 (3)

TABLE 7 Summary of Coutada 11's anti-poaching statistics between 2017 and 2021.

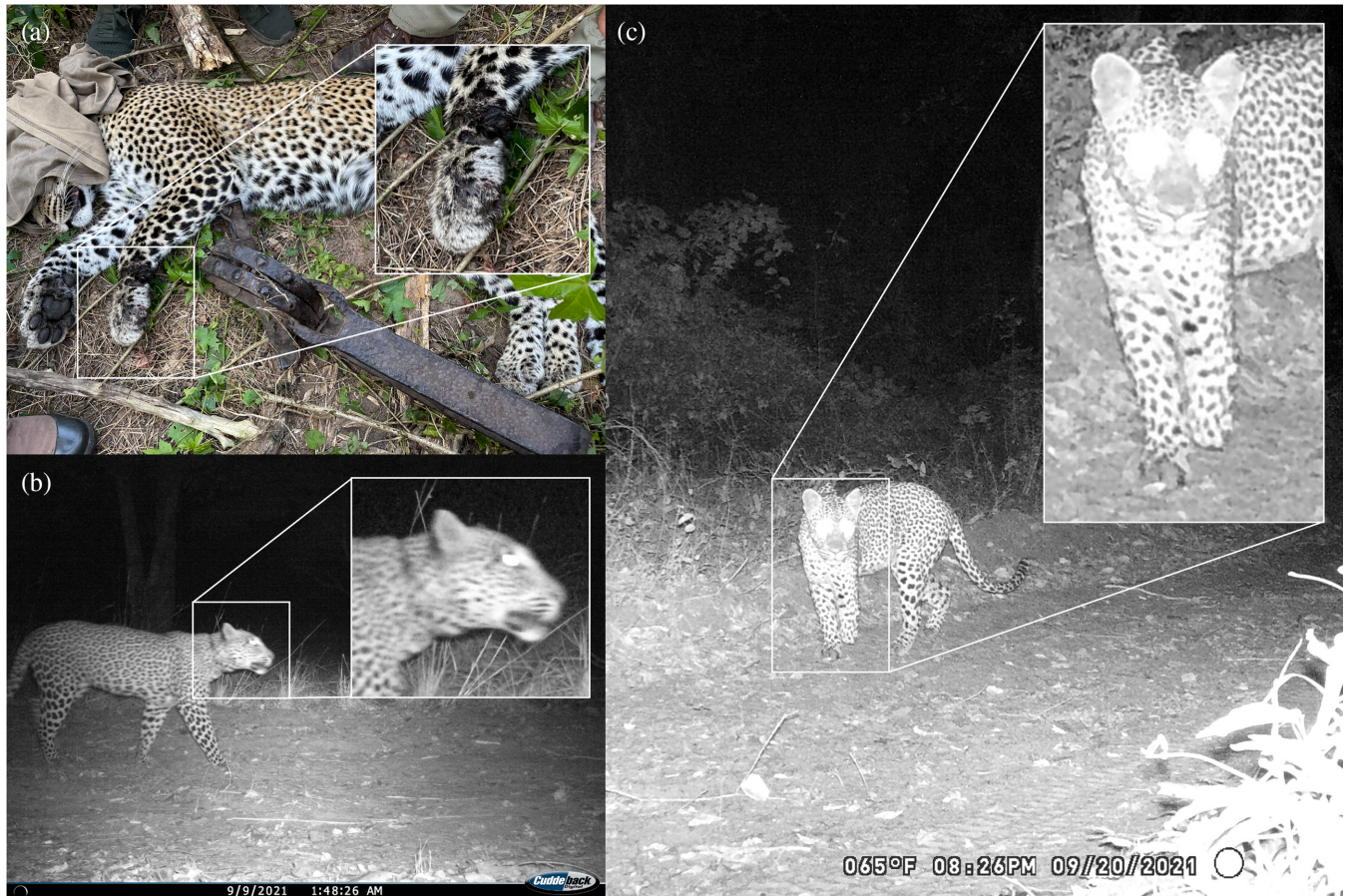| Year	Poachers arrested	Snares removed	Gin traps removed
2017	124	5897	347
2018	54	1975	63
2019	63	969	82
2020	57	678	176
2021	61	702	108

FIGURE 4 Photographic evidence of leopards affected by wire snares and gin traps in the Zambezi Delta between 2019 and 2021. A = female leopard found in a gin trap; B = female leopard with a snare wound around the neck; C = female leopard with a missing foot from a gin trap.

impact leopard density due to high mortality rates, with these areas functioning as population sinks, and the resulting edge effects may lead to population declines or extirpations (Balme et al., 2010; Havmøller et al., 2019; Rosenblatt et al., 2016). A growing body of evidence showing how anthropogenic impacts inside and surrounding PAs (Naude, Balme, O'Riain, et al., 2020; Rogan et al., 2022) or WMAs (Loveridge et al., 2022) limit regional leopard populations. In contrast, human activity index and distance to community did not appear to affect leopard detectability and density in the study, respectively. However, given the scarcity and inconsistency of scalable human activity data throughout the landscape,

the lack of any measurable effect should not be interpreted as the absence thereof. Furthermore, these human-related covariate effects were potentially masked by the "buffered" study area and relatively low human density in the WMAs. While leopard trophy hunting in the Delta is well-managed and funds anti-poaching efforts, and encroachment of human activity within WMAs is regulated, bushmeat poaching has only recently been brought under control by gradually increased and sustained anti-poaching efforts.

Trophy hunting of large carnivores has the potential to generate significant financial returns for conservation (Lindsey et al., 2007, 2012), while poorly managed

hunting may drive population declines and ultimately imperil both the industry and the conservation revenue it provides (Loveridge et al., 2007; Muller et al., 2022; Packer et al., 2011). Leopards are particularly sensitive to over-harvest due to their complex social systems and reliance on relatively stable kin-clustering (Fattebert et al., 2016). Over-harvest may promote high turnover and immigration rates of adult males which can increase intraspecific competition, facilitate infanticide, and promote inbreeding (Balme, Slotow, & Hunter, 2009; Naude, Balme, O'Riain, et al., 2020; Packer et al., 2009). Mozambique only allocates trophy hunting quotas for adult male leopards, which account for approximately 14% of industry income nationally (Lindsey et al., 2012). Currently, these quotas are based on the Martin and de Meulenaer (1988) density estimate of 10 leopards/100 km^2 (MITADER, 2018), which has been heavily criticized (Balme et al., 2010; Norton, 1990) for over-estimating leopard density across Mozambique. This model does not account for important factors such as anthropogenic mortality, assuming that leopards occur at optimal densities across all available habitats (Strampelli et al., 2018). In 2007, this model (Martin & de Meulenaer, 1988) justified the doubling of national leopard trophy hunting quotas in Mozambique to 120 leopards per annum; however, export tags issued from 2006 to 2010 and 2011 to 2017 were only ~30% and ~50% of annual quotas, respectively (Braczkowski et al., 2015; MITADER, 2018). While trophy hunting quotas should ideally be based on robust density estimates (Braczkowski et al., 2015), these are lacking across their range. Where such estimates do exist, this study joins mounting evidence suggesting that current leopard densities in Mozambique are substantially lower than those predicted by Martin and de Meulenaer (1988). Thus, we reiterate the need for an evidence-based and locally relevant reevaluation of the leopard trophy hunting quota system in the country. In recent years, legal hunting quota allocations in the Delta have remained relatively consistent and low for the entire contiguous landscape (i.e., 0.41 leopards/1000 km^2, Table 6), with no quota issued for Coutada 14 and the cessation of hunting in Coutada 12 from 2017. This limited quota and recent offtake in the Delta could be considered sustainable, remaining well below the suggested annual hunting quota of 1.0 leopards/1000 km^2 in more comparable Tanzanian landscapes (Packer et al., 2011). However, considering the WMAs (Coutada 10 and 11) where leopards are trophy hunted in isolation, current leopard quotas are likely set at the maximum harvest limit (1.00 and 1.04 leopards/1000 km^2, respectively), and accounting for concurrent impact of illegal offtake, these quotas likely breach sustainable levels (Jorge et al., 2013). Under the current evidence of sustained offtake, a moratorium

on hunting might be considered until the population recovers; however, such drastic regulations may compromise the financial stability of operators in these WMAs which may have unintended consequences for biodiversity conservation, and as such, a quota reduction (preferably by 50%) should be introduced until longitudinal trend data are available for more appropriate quota allocation.

Bushmeat poaching is widespread and poses a direct threat to large carnivore populations (Lindsey et al., 2013); however, few studies have reported the extent and frequency of such illegal offtake across leopard range (Becker et al., 2013; Gubbi et al., 2021; Loveridge et al., 2020; Swanepoel et al., 2015; Williams et al., 2017). While leopard adaptability ostensibly provides greater resilience to such anthropogenic threats (Burton et al., 2012), low reproductive rates and slow generational turnovers often limits demographic recovery (Jacobson et al., 2016), especially under protracted human pressure (Loveridge et al., 2022; Rogan et al., 2022). Historically, leopards were targeted in the region to supply an external skin trade (Maugham, 1914) and there remains an ongoing targeted demand both locally (Everatt et al., 2019) and regionally (Naude, Balme, Rogan, et al., 2020). Leopards are particularly susceptible to indiscriminate poaching methods and are often caught as bycatch (Fattebert et al., 2013). In Murchison Falls National Park in Uganda, high snaring density (0.08–4.58 snares/km^2) was suggested as the limiting factor for large carnivores as their populations were kept at artificial asymptotes due to substantial by-catch despite concurrent increases in ungulate populations (Mudumba et al., 2021). Three individually identified leopards were visibly affected by poaching in the 2021 survey. While this likely underestimates actual impact (Becker et al., 2013; Loveridge et al., 2020; Mudumba et al., 2021), it does suggest that poaching remains a major threat to this leopard population, despite recent anti-poaching success (Table 7). Currently, wire snares and gin traps are the most frequently used bushmeat poaching techniques in central Mozambique (Lindsey et al., 2013) and have most likely contributed to the limited postwar recovery of this leopard population, reaffirming a pervasive theme for large carnivores across the country (Bouley et al., 2018; Everatt et al., 2019; Lindsey et al., 2013; Lindsey & Bento, 2012).

Population density estimation, determining prey-based carrying capacity and quantifying anti-poaching effort pose several caveats and limitations. Landscape heterogeneity prevents extrapolation across the Delta, as the camera trapping design was limited to the central WMA which is "buffered" against anthropogenic pressures by surrounding WMAs and Marromeu National

Reserve, thus leopard density estimates likely represent a "best-case" scenario across the Delta. While aerial counts are an effective and widely accepted means of estimating medium- to large-bodied ungulates in open to semi-open habitats, applying these methods in closed canopy forests can underestimate abundance (Jachmann, 2002). Prey-based leopard carrying capacity estimates were also limited by the lack of site-specific dietary preferences; here, alternative prey preferences from a nearby PA were used for local applicability (Briers-Louw & Leslie, 2020). While anti-poaching patrols aim to minimize poaching activity systematically throughout the landscape, efforts typically respond to areas of increasing snare detection, thus quantification of poaching trends may be confounded over time (Becker et al., 2013; Kendon et al., 2022; Loveridge et al., 2020). Despite these potential methodological caveats, this site-specific leopard density estimation provides a novel baseline for the region. As both aerial prey counts and anti-poaching efforts have remained constant over time, such limitations are tolerable in order to contextualize our understanding ecological capacity and anthropogenic pressure.

Armed conflict can be a significant threat to large carnivore populations and may lead to local extinctions (Atkins et al., 2019; Bauer et al., 2022; Stevens et al., 2011); however, rapid intervention and long-term conservation efforts in post-conflict landscapes may facilitate population recovery (Daskin & Pringle, 2018). For instance, the cessation of armed conflict in Mozambique and Angola, coupled with improved conservation efforts have resulted in population recoveries of lion and leopard, respectively (Bouley et al., 2018; Braga-Pereira et al., 2020). Such recovery will, however, remain limited without effective protection and long-term management of unsustainable anthropogenic mortality, as observed in Cambodia where unregulated poaching postwar culminated in a 72% density decline of a recovering leopard population (Gray & Prum, 2012; Rostro-García et al., 2018). Similarly, the Delta was subjected to decades of war and sustained anthropogenic pressure on both prey and carnivore populations. While prey populations are continuously recovering naturally postwar (Beilfuss et al., 2010; Macandza et al., 2022), the comparatively low leopard density estimates indicate that the population is far from secure. However, the small, but meaningful differences between the single- and multi-session density estimates suggest that the leopard population may be increasing, although these could conversely be explained by differences in sampling effort and bias. Nevertheless, there is clearly scope for recovery provided that increased conservation efforts continue to restrict illegal killings of leopards throughout the landscape. The recent reintroduction of leopards into Gorongosa National Park,

and the presence of leopards in adjacent forestry concessions (Easter et al., 2019) and wildlife and community management areas (Lindsey & Bento, 2012; Stein et al., 2020), increases the potential for population connectivity and recovery across central Mozambique.

We argue that leopard density estimates in Coutada 11 are lower than expected, given available literature and comparable study sites. We then consider ecological limitations and exclude habitat, prey and competitors as both habitat and prey are suitable and available for leopards, with little or no evidence of competing carnivores. We then consider anthropogenic limitations, where we first argue that the relatively well-managed, low-volume, consistent, and selective nature of trophy hunting in the Delta means that while this legal offtake is certainly having an effect on the extant leopard population, this could be justified given that actual offtake is well below comparable literature-derived sustainable offtake levels (Packer et al., 2011) and that the benefits of WMAs, such that it is primarily financed and secured by hunting, maximizes conservation value over alternative and currently infeasible or unsustainable protection models in the Delta. We then argue that what remains is illegal offtake (i.e., non-selective and unsustainable bushmeat poaching) as a well-established and likely agent of leopard population suppression instead of the expected postwar recovery. We postulate that while bushmeat poaching has been restricted throughout the landscape with increasing success over the past 5 years, the very scale and progressive effort required to keep this at bay is evidence of the illegal poaching pressure on the landscape that would otherwise be rampant and arguably more destructive than it already is (see Table 7). Anecdotally, we also offer evidence of visible snaring on camera traps as further, but by no means comprehensive, evidence of this effect, highlighting that the very nature of the crime inherently makes it difficult to measure, thus we rely on proximate measures of its effect in the landscape.

Both legal and illegal offtake of leopards can cause detrimental impacts on local populations, even within relatively short timeframes (Loveridge et al., 2020; Packer et al., 2011; Williams et al., 2017), thus follow-up monitoring in the Delta would be crucial to quantifying population trends. Such studies could aid adaptive management of the Delta landscape directly by responding to density changes. If density: (i) increases, management should maintain the *status quo*; (ii) remains stable, management should focus efforts on further decreasing illegal poaching pressure; and (iii) decreases, more drastic measures should be taken (e.g., introduction of new protection efforts, temporary full exclusion, and even consider a temporary moratorium on legal leopard trophy hunting). The goal is not to disadvantage the

trophy hunting industry or prevent the consumptive use of leopards, especially since the ban on trophy hunting will exacerbate biodiversity loss (Di Minin et al., 2016) and could be detrimental to the local and national economy (Jorge et al., 2013). Fundamentally, the viability of the industry hinges on maintaining and facilitating recovery of wildlife populations to increase conservation funding and ensure that revenue lasts in order to promote conservation efforts. Additionally, providing tangible benefits to local communities living alongside wildlife to reduce dependency on illegal bushmeat poaching is paramount, and has been incorporated into the Coutada 11 conservation model through construction and support of a school and clinic, establishment of bee-keeping and fishing projects, provisioning of agricultural fields and consistent ethically sourced meat supplementation among other initiatives. Furthermore, of the national conservation estate in Mozambique, WMAs account for approximately double (17%) that of PAs (8%; Booth, 2012), while income generated from trophy hunting is typically reinvested into the landscapes by funding anti-poaching and management activities, while supporting local communities and government initiatives (Jorge et al., 2013; Lindsey et al., 2007). Thus, we rather use this objective evidence-based approach to identify gaps in knowledge and present information to equip managers and policymakers toward improving active management and long-term conservation of leopards.

AUTHOR CONTRIBUTION STATEMENT

ACKNOWLEDGMENTS

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Supplementary files will be made available online.

ETHICS STATEMENT

This research abided by the Code of Ethics of the Society for Conservation Biology, having been conducted under a research permit (ANAC RP# 06-10-2023) from the National Administration of Conservation Areas (ANAC) in Mozambique. Permission was obtained from the concessionaire of Coutada 11 to conduct the camera trap research on this wildlife management area. The research design did not require ethical approval from the principal investigator's institution as camera traps are a non-invasive technique and the cameras used in this study did not use flash.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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