Density responses of lesser-studied carnivores to habitat and management strategies in southern Tanzania's Ruaha-Rungwa landscape

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Abstract

Compared to emblematic large carnivores, less charismatic or smaller carnivore species often receive little conservation attention, despite facing increasing anthropogenic pressure, and their status being poorly understood across much of their range. We employed systematic camera trapping and spatially explicit capture-recapture modelling to estimate variation in population density of serval, striped hyaena and aardwolf across the mixed-use Ruaha-Rungwa landscape in southern Tanzania. Three sites were selected as representative of different habitat types, management strategies, and levels of anthropogenic pressure: Ruaha National Park's core tourist area, dominated by *Acacia-Commiphora* bushlands and thickets; the Park's miombo woodland; and the neighbouring community-run MBOMIPA Wildlife Management Area, also covered in *Acacia-Commiphora*.

Our results show that the Park's miombo woodlands supported a higher serval density than the core tourist area and Wildlife Management Area, with 5.56 [Standard Error = ±2.45], 3.45 [±1.04] and 2.08 [±0.74] individuals per 100 km^2, respectively. This variation is likely driven by precipitation, the abundance of apex predators, and the level of anthropogenic pressure.

Striped hyaena were detected only in the Wildlife Management Area and at low density (1.36 [±0.5] individuals per 100 km^2), potentially due to the location of the surveyed sites at the edge of the species' global range, high densities of sympatric competitors and anthropogenic edge effects.

Finally, aardwolf were captured in both the Park's core tourist area and the Wildlife Management Area, with a higher density in the Wildlife Management Area (13.25 [±2.48] versus 9.19 [±1.66] individuals per 100 km^2), possibly as a result of lower intraguild predation and late fire outbreaks in the area surveyed.

By shedding light on three understudied African carnivore species, this study highlights the importance of miombo woodland conservation and community-managed conservation, as

well as the value of camera trap data to improve ecological knowledge of lesser-known carnivores.

Introduction

Emblematic large carnivores often benefit from significant conservation investment and are prioritised in terms of resource allocation over more threatened species [1]. Such prioritisation stems in part from their essential role in shaping ecosystems [2], but also their charisma and cultural significance, which are used to highlight the problem of biodiversity loss to the public [3,4]. In comparison, carnivores with smaller body size or less appeal tend not to spark as much conservation interest and remain understudied globally [1,5]. This imbalance is conspicuous in the African conservation landscape, where iconic apex predators such as lion (*Panthera leo*), leopard (*Panthera pardus*) and cheetah (*Acinonyx jubatus*) have drawn much research attention [6]. Overshadowed by these flagship species, many lesser-studied carnivores are nonetheless facing declining trends in number and range [7], with anthropogenic threats such as habitat loss and fragmentation [8], and persecution [9] jeopardising their survival alongside a growing human population [10].

This lack of research hinders conservation status assessments for a number of African carnivores, thus precluding effective conservation planning [11], notwithstanding the ecological importance and vulnerability to extinction of many of these species. For instance, striped hyaena (*Hyaena hyaena*) have received very little conservation attention across their African range, although they provide essential ecosystem services in consuming carcasses and dispersing their nutrients [12]. The species is thought to be declining globally, mainly caused by poisoning and decreasing sources of carrion, leading to its classification as "Near Threatened" [13]. Population status information is also lacking for many mesocarnivores, despite their important contribution to regulating lower trophic levels and maintaining biodiversity [14]. Classified as "Least Concern", serval (*Leptailurus serval*) and aardwolf (*Proteles cristata*) are nevertheless facing increasing pressure due to continued urbanisation

73 and agricultural expansion [15,16]. Serval are particularly vulnerable to the degradation of

74 wetland and grassland habitat, as the species preferentially uses well-watered environments

75 which attract higher densities of small mammals [17]. The insectivorous diet of the aardwolf

76 exposes the species to insecticide poisoning, a threat which is likely to grow with the

77 intensification of agriculture [15,18].

78 The IUCN recommends further research to bridge knowledge gaps for these lesser-

79 studied carnivore species' spatial ecology and population status [13,15,16]. The distribution of

80 serval, striped hyaena and aardwolf, as well as population abundances and densities across

81 their range, need to be investigated and accurately estimated to inform effective management

82 strategies and conservation planning [19]. The cryptic nature of these species often impedes

83 direct observation, and camera trapping offers a more efficient alternative in collecting data

84 [20]. Over the past decade, spatial capture-recapture [21], a well-established method for

85 estimating the density of species with individual markings such as patterned coats, has been

86 successfully used to assess population density of these three carnivore species. Most of the

87 published estimates for striped hyaena, however, concern Asiatic populations [22-24], with a

88 single study of an African population from Kenya [25]. Spatial capture-recapture studies of

89 aardwolf density are similarly limited, with only two published estimates from Kenya and

90 Botswana [25,26]. While density studies dedicated to serval have been carried out in Southern

91 Africa [26-29], and Western and Central Africa [30,31], no spatial capture-recapture estimates

92 currently exist for any East African population.

93 Tanzania's Ruaha National Park (RNP) is the second largest National Park in East

94 Africa, at over 20,000 km^2, and corresponds to the southern range limit for both the global

95 striped hyaena population and the East & Northeast African aardwolf population [13,15]. RNP

96 belongs to the greater Ruaha-Rungwa landscape, which harbours important wildlife

97 biodiversity, partly due to the convergence of *Acacia-Commiphora* and miombo woodland

98 (*Brachystegia-Jubelnardia*) ecotypes [32]. The Ruaha-Rungwa landscape also encompasses

99 a range of fully and partially protected areas, including Game Reserves, Game Controlled

100   Areas, Open Areas, and community-managed Wildlife Management Areas (WMA).

101   Established on communal lands, WMAs are one of the most novel features in Tanzania's

102   conservation landscape and are intended to promote a sustainable scheme involving local

103   communities in wildlife protection and its economic benefits [33]. Carnivores in the Ruaha-

104   Rungwa landscape are exposed to multiple types and levels of anthropogenic pressure,

105   including habitat conversion for agriculture, prey base depletion due to bushmeat poaching,

106   and direct persecution by humans in retaliation to livestock predation [34,35].

107   Our goal was to provide baseline status estimates in this landscape for three African

108   carnivore species for which data are currently lacking, and in doing so assess the impact of

109   different habitats, management strategies and levels of protection and anthropogenic pressure

110   on their population densities. We used camera trapping and spatially explicit capture-

111   recapture (SECR) modelling [36] to estimate population densities of serval, striped hyaena

112   and aardwolf at three sites in Ruaha-Rungwa, representative of different ecosystem types and

113   levels of protection and anthropogenic pressure: the *Acacia-Commiphora* core tourist area of

114   RNP; the miombo woodland of western RNP; and the community-run *Acacia-Commiphora*

115   MBOMIPA WMA, which adjoins Ruaha to the east and acts as a buffer between the Park and

116   unprotected village lands.

Materials and methods

Ethics statement

119   Data collection consisted of camera trapping, a non-invasive method which does not

120   involve contact with the study species and minimises interferences with their natural

121   behaviour. Fieldwork was carried out under research permits 2018-368-NA-2018-107 and

122   2019-424-NA-2018-184, granted by the Tanzania Commission for Science and Technology

123   (COSTECH) and Tanzania Wildlife Research Institute (TAWIRI).

Study area

The Ruaha-Rungwa ecosystem in southern Tanzania spreads over 45,000 km^2 across three ecoregions: Central Zambezian miombo woodlands, Eastern miombo woodlands, and Eastern African acacia savannas [37] (Figs 1A-B). Ruaha National Park lies at the centre of this ecosystem and was the largest National Park in Tanzania until the formation of Nyerere National Park in 2019 [38]. With an altitude ranging from 716m to 1,888m [39], the terrain features low rolling hills overlooked by an escarpment to the north, and the Great Ruaha River runs along the RNP's eastern border [40]. RNP experiences a semi-arid to arid climate and a unimodal rainfall regime, from December to April [41]. *Acacia-Commiphora* deciduous bushlands and thickets predominate in about two-thirds of the park, while miombo woodlands cover its western part [42] (Fig 1B). The Ruaha-Rungwa landscape is completed by a number of Game Reserves, Game Controlled Areas and Open Areas bordering RNP to the north and the west, and by the Matumizi Bora ya Malihai Idodi na Pawaga (MBOMIPA) and Waga WMAs, stretching along its eastern border. MBOMIPA WMA was established in 2007 based on the principles of community-based natural resource management [33] and is subject to greater levels of anthropogenic impacts than the core tourist area of RNP [43]. This landscape is unfenced, which facilitates free movement of wildlife.

Fig 1. Ruaha-Rungwa landscape and spatial distribution of camera trap stations. (A) Location of the Ruaha-Rungwa landscape in Tanzania. (B) Ruaha-Rungwa landscape's ecotypes and land uses. Boundaries of additional protected areas are depicted on the map, but not named. Only villages and towns near protected areas are shown. (C) Core RNP *Acacia-Commiphora* grid. (D) RNP miombo grid. (E) MBOMIPA WMA *Acacia-Commiphora* grid.

Camera trap surveys

The study used a photographic dataset collected between June and November 2018 in RNP and MBOMIPA WMA to assess the status of leopard [43]. Two sites were surveyed within

150 RNP, and one in MBOMIPA WMA (Figs 1C-E). The first camera trap grid covered an area of

151 223 km^2 in highly-productive riverine *Acacia-Commiphora* habitat [44], at the core of the park's

152 tourist area, with 45 camera stations set out for 83 days. The second grid, located in miombo

153 woodland in the western part of RNP, consisted of 26 camera stations over an area of 152

154 km^2 for 90 days. A third grid was conducted in highly-productive riverine *Acacia-Commiphora*

155 habitat in MBOMIPA WMA, with 40 stations spanning a total area of 270 km^2 for 69 days.

156 The duration of each survey was kept below 90 days to minimise potential violations of

157 the assumption of demographic closure, as per previous studies [20,45]. The design of camera

158 trap layout sought to optimise capture rate of large carnivores, facilitate individual

159 identification, and ensure no gaps in the trapping array. Camera placement prioritised roads

160 and junctions, or game trails, as large carnivores preferentially travel along roads [46]. With a

161 single road crossing the study area within the park's miombo woodland, half of the cameras

162 in the RNP miombo grid were set on game trails along semi-open *mbugas* (drainage lines).

163 The mean distance between two cameras ranged from 1.88 km in RNP miombo to 1.96 km

164 and 2.08 km in Core RNP *Acacia-Commiphora* and WMA *Acacia-Commiphora*, respectively.

165 All but one of the stations consisted of paired cameras facing one another on either side

166 of a road or trail, to increase the likelihood of capturing both flanks of passing animals [45].

167 Cameras were mounted on trees at approximately 40cm height, with the surrounding

168 vegetation regularly cleared to prevent any obstruction of the lens or sensor and reduce the

169 risk of bush fire damaging the camera. The survey deployed several motion-activated camera

170 models: Cuddeback Professional Color Model 1347 and Cuddeback X-Change Color Model

171 1279, Non Typical Inc., Wisconsin, USA; HC500 HyperFire, Reconyx, Wisconsin, USA. The

172 majority of cameras were equipped with xenon flashes, which produce higher definition

173 images of animal markings than infrared LED flashes [47].

Density estimation

175   We estimated the population density (defined as the number of individuals per 100 km^2)

176   of serval, striped hyaena and aardwolf at each survey site via Maximum Likelihood Estimation

177   SECR analysis, with the package secr v3.2.0 [48] in R version 3.6.3 [49]. SECR combines two

178   sub-models representing the spatial distribution of a population and the detection process

179   respectively [50], and therefore does not require ad hoc estimation of the effective trapping

180   area as per conventional capture-recapture methods [51].

181   Data inputs consisted of detection histories detailing sampling occasions and locations

182   of captures for each individual throughout the survey, and a trap layout, listing the coordinates

183   of every camera trap station and their activity periods (S2-S3 Appendixes). Individuals were

184   identified from camera trap images through their unique pelage markings [45], focusing on

185   flanks for serval and fore-quarters and hind-quarters for striped hyaena and aardwolf, as

186   shown in S1 Appendix. Detection histories were produced using the flank with the greatest

187   number of capture events for each species and grid using the following framework: (i) sampling

188   occasions were set to 24-hours from midday to midday, to account for the nocturnal nature of

189   the studied species; (ii) individuals could be recorded at different locations during a sampling

190   occasion, but only once per given location (as per standard practice; [52]).

191   The SECR observation sub-model describes the individual detection probability as a

192   monotonous function of the distance to home range centre, characterised by g0, the detection

193   probability at the range centre, and σ, a spatial scale related to home range width [53]. We

194   tested three standard functions (half-normal, negative exponential and hazard rate) to model

195   the decrease of the detection function with the distance to the home range centre. To minimise

196   any bias in estimated densities, we selected a buffer width at which density estimates reached

197   a plateau for each analysis.

198   We tested for variation in the baseline encounter probability g0 through the use of

199   embedded predictors and covariates hypothesised to influence detection probability [54].

200   Specifically, we investigated the behavioural response of individuals to capture events by

201   fitting the global trap response model (b predictor) and the local trap response model (bk

202   predictor), and assessed the influence of the type of flash at each station (xenon versus LED

203   flash), and station location (on-road versus off-road) on detection. Finally, we examined the

204   effect of sex on detection function parameters g_0 and σ by fitting a hybrid mixture model, which

205   accommodates individuals of unknown sex [55]. Model selection was carried out by ranking

206   models based on their Akaike Information Criterion score, corrected for small sample size

207   (AICc) [56]. When more than one candidate model had substantial empirical support (ΔAICc

208   < 2) [56], a final density estimate was derived by applying model averaging based on AICc

209   weights [21].

Results and discussion

Results

Survey effort

213   The sampling effort across the 111 stations deployed at the three study sites totalled

214   8,477 camera trap nights and yielded 226 images of serval, 125 images of striped hyaena and

215   1,119 images of aardwolf (see S4 Appendix). Individual identification could be carried out for

216   86.3% of serval photographs, 72.8% of striped hyaena photographs, and 81.1% of aardwolf

217   photographs. Detection histories for serval featured 38 independent capture events for 13

218   identified individuals in Core RNP *Acacia-Commiphora*, 31 events for 10 identified individuals

219   in WMA *Acacia-Commiphora*, and 23 events for 12 identified individuals in RNP miombo.

220   Striped hyaena were captured in WMA *Acacia-Commiphora* only, with 42 independent capture

221   events and 12 identified individuals. Aardwolf were captured in Core RNP *Acacia-*

222   *Commiphora* and WMA *Acacia-Commiphora* only, with 36 and 37 individuals identified,

223   accounting for a total of 240 and 185 independent capture events, respectively.

224   Aardwolf displayed the highest recapture rate, i.e. the percentage of individuals captured

225   more than once, across all grids (84.9%), followed by striped hyaena (58.3%) and serval

226   (57.1%). All captured individuals were adults or subadults, with the exception of one female

227   serval and one aardwolf accompanied by offspring. The target species showed predominantly

228   nocturnal activity, with 86% of identified serval captures, 98% of striped hyaena captures, and

229   99.4% of aardwolf captures occurring between 7 pm and 6 am. The poor visibility of genitalia

230   and lack of clear secondary sexual traits limited sex determination to 2.9% of the identified

231   servals and 16.7% of identified striped hyaenas, making it impossible to model sex differences

232   in the density estimation process. Aardwolf sexing was more successful, with sex assigned to

233   35.6% of identified individuals, which allowed sex difference modelling in density estimation.

Population density

235   Of the three detection functions tested, the negative exponential function best fitted the

236   datasets for all target species in the three sites. We found no evidence of learned behavioural

237   response or influence of covariates on detection for serval in Core RNP *Acacia-Commiphora*

238   and WMA *Acacia-Commiphora*. On the other hand, the model in which g0 varied with station

239   location was supported in RNP miombo. Ranking results based on AICc score are detailed in

240   S5 Appendix. The highest serval density was obtained in RNP miombo, with 5.56 [Standard

241   Error = ±2.45, Confidence Interval = 2.44-12.69] individuals per 100 km^2, followed by 3.45

242   [±1.04, 1.93-6.16] individuals per 100 km^2 in Core RNP *Acacia-Commiphora,* and 2.08 [±0.74,

243   1.05-4.09] individuals per 100 km^2 in WMA *Acacia-Commiphora* (Fig 2, and see Table 1 for

244   parameters g0 and σ).

245   For striped hyaena in WMA *Acacia-Commiphora*, two models received strong support

246   (∆AICc < 2, [56]); the model with constant g0 and sigma, and the local trap response model

247   (bk). Model averaging returned an estimated density of 1.36 [±0.50, 0.68-2.72] individuals per

248   100 km^2.

249   For aardwolf in Core RNP *Acacia-Commiphora,* learned behavioural response

250   influenced capture probability, with the local trap response model (bk) ranking highest, while

251   the models in which g0 or sigma varied with sex ranked highest in WMA *Acacia-Commiphora*.

252   Aardwolf density was estimated at 9.19 [±1.66, 6.46–13.06] individuals per 100 km^2 in Core

253   RNP *Acacia-Commiphora,* and 13.25 [±2.48, 9.22–19.05] individuals per 100 km^2 in WMA

254   *Acacia-Commiphora*.

255   **Fig 2**: **Population density estimates for the target species at the three survey sites.** Bars

256   represent standard errors.

257   **Table 1. Detection probability parameter estimates and standard errors for the target**

258   **species at the three survey sites.** Predictor bk-= 1 for site-specific step change after the first

259   capture.

Species	Site	Predictor	Estimate ± SE	
			g0	σ(m)
Serval	Core RNP *Acacia-Commiphora*		0.041 ± 0.014	1062 ± 171
	RNP miombo	On road	0.033 ± 0.017	1249 ± 361
		Off road	0.006 ± 0.004	
	WMA *Acacia-Commiphora*		0.034 ± 0.013	1566 ± 299
Striped hyena	WMA *Acacia-Commiphora*	bk=0	0.032 ± 0.016	2625 ± 521
		bk=1	0.078 ± 0.029	
Aardwolf	Core RNP *Acacia-Commiphora*	bk=0	0.030 ± 0.009	1220 ± 131
		bk=1	0.263 ± 0.038	
	WMA *Acacia-Commiphora*	Female	0.135 ± 0.085	476 ± 111
		Male	0.323 ± 0.075	553 ± 42

260

Discussion

Density comparison

263   This study produced the first population densities estimated through spatial capture-

264   recapture for three lesser-studied carnivores, serval, striped hyaena and aardwolf, in

265 Tanzania. Using camera trap data from the Ruaha-Rungwa landscape, we shed light on the

266 population density responses of these increasingly threatened species to habitat and land

267 management strategies. Our results provide an important baseline and reference estimate

268 that can be employed to assess and monitor the status of striped hyaena, aardwolf and serval.

269   Serval densities were higher within the RNP grids than in WMA *Acacia-Commiphora*,

270 and in particular within the miombo woodland. This density distribution follows the precipitation

271 pattern over the Ruaha-Rungwa landscape, as the miombo woodlands in the south-western

272 part of RNP receive the greatest amount of rainfall on average and WMA *Acacia-Commiphora*

273 is the driest of the three surveyed areas [41]. The miombo woodlands feature open, grassy

274 *mbuga* ("dambo") drainage lines. Mbugas are seasonally flooded, and water remains present

275 year-round, usually in distinct springs or pools rather than streams during the dry season. This

276 result aligns with the preference of servals for well-watered environments, such as wetlands

277 and riparian habitat [17]. The difference between RNP miombo and Core RNP *Acacia-*

278 *Commiphora* could also stem from the lower abundance of lion, leopard and spotted hyaena

279 in the miombo woodlands [43], as these apex predator species have been recorded to

280 occasionally kill serval [57]. The lower serval population density in WMA *Acacia-Commiphora*

281 likely results from the WMA's proximity to unprotected land, inducing greater edge effects [58],

282 and a more pronounced level of anthropogenic pressure. For instance, the camera stations in

283 the WMA recorded nine illegal incursions, two of them with evidence of bushmeat hunting, as

284 well as two spotted hyaenas and two striped hyaenas bearing marks of snare captures. The

285 common use of dogs for bushmeat hunting may also negatively impact resident populations

286 of serval, as occasional killings by domestic dogs have been observed elsewhere in Tanzania

287 [59]. In contrast, evidence of only one illegal incursion was recorded in the RNP grids over the

288 duration of the survey. Moreover, the lower abundance of small ungulates in the WMA due to

289 anthropogenic impacts and the lack of habitat immediately outside the WMA may intensify

290 competition between serval and leopard [44]. In areas with fewer impalas or other medium-

sized antelopes, leopard may shift their diet towards smaller prey species, such as large rodents and birds, and thus increase their dietary overlap with serval [60].

Serval density estimates using spatial capture-recapture vary greatly across Africa, from 0.63 and 1.28 individuals per 100km^2 in northern Namibia [28] to 101.21 in Mpumalanga, South Africa [29]. The latter estimate comes from a heavily modified habitat where the absence of persecution and interspecific competition, combined with high rodent biomass, enables serval to attain such high numbers. In comparison, our results lie within the lower range of published densities and are close to estimates for the Niokolo Koba National Park, Senegal (3.49 - 4.08 individuals per 100 km^2) [31] and the Drakensberg Midlands, South Africa (6.0 - 8.3 individuals per 100 km^2) [27]. The only other density estimate available for the species in Tanzania exceeds our results, with 10.9 [SE = 3.17] individuals per 100 km^2 in Tarangire National Park [61]; however, the study employed conventional capture-recapture, which has been shown to overestimate density compared to spatial capture-recapture [62].

We could only estimate striped hyaena population density in WMA *Acacia-Commiphora*, as the camera trap survey did not detect any individuals in Core RNP *Acacia-Commiphora* or RNP miombo. The Ruaha-Rungwa landscape lies at the southern limit of the species' global range [13]; deeper within the species' range, in Laikipia County, Kenya, population density estimated through SECR was around six times higher than the density estimated in WMA *Acacia-Commiphora* [25]. Such a pattern is consistent with widespread biogeographic trends, typically showing diminished abundance towards species range edges [63]. Furthermore, the species is closely associated with *Acacia-Commiphora* bushland within Africa [59], and the fact that our study landscape traverses a transition from this habitat to miombo woodland may point to a mechanism delimiting the range edge in this area. The low density observed in WMA *Acacia-Commiphora* may also ensue from high edge effects due to the area's proximity to human-dominated areas [58], as highlighted by the record of two individuals showing evidence of wire snare capture during the study period.

In contrast to serval, we estimated a higher aardwolf density in WMA *Acacia-Commiphora* than in Core RNP *Acacia-Commiphora*. The difference probably results from milder intraguild predation in the WMA, which supports lower densities of apex predators than the core tourist area of RNP [43]. Moreover, as aardwolf primarily feed on harvester termites, depletion of ungulates would not trigger dietary overlap with larger carnivores [18]. In addition, aardwolf may benefit from accidental fire outbreaks which often occur later in the dry season in the WMA; the reduced grass cover caused by this burning may force harvester termites to range more widely in search of food, thus lengthening their exposure time to predation on the ground [64,65]. The reverse trend in aardwolf density compared to serval could indicate different sensitivities to anthropogenic pressures between the two species, although poaching activities in the area do not specifically target either species. Aardwolf may also be more prone to predation by apex predators, with greater stealth and agility giving serval an edge on the slower-moving aardwolf when threatened [17]. The absence of records of aardwolf in miombo woodland reflects the species' known preference for *Acacia–Commiphora* bushland [59]. Our results align with aardwolf population densities estimated through conventional capture-recapture and spatial capture-recapture in Tarangire National Park and Kenya's Laikipia District, of 9.04 and 11.63 individuals per 100 km^2, respectively [61,25].

Camera trap location impacted detection probability for serval in RNP miombo. Rather than denoting serval's preference for larger roads, the higher detection probability at stations located on roads probably results from the particular road network in this portion of RNP, consisting of a single road complemented by numerous subsidiary game trails. Though we tried to select the most heavily used trails, their large number offers wildlife multiple equivalent options compared to the stations set on the most readily accessible road. For aardwolf in Core RNP *Acacia-Commiphora* and striped hyaena, the probability of detection at a camera trap station was higher for individuals that had already been captured at the same site. This suggests individuals favouring the core area of their home range more often than the periphery, and not being deterred by camera trap flashlights (xenon or LED flash). Sex

appeared to have a mild impact on aardwolf capture probability in WMA *Acacia-Commiphora*, with males having a higher probability of capture than females.

Conservation implications and recommendations

We used a photographic dataset from a research project targeting leopard. Considering the logistical and budget requirements of camera trapping, this study illustrates the value of by-catch data in terms of resource optimisation, provided that the survey design also complies with the ecology of the non-target species [66]. In this study, the conservative trap layout with an average distance between stations of around 2 km was compatible with the home ranges of the species we considered [67,68], and allowed individuals' recapture at multiple camera trap stations [69]. However, the trap layout configuration was tailored to maximise leopard capture rate, with stations preferentially deployed on roads and junctions [46], which may not be optimum for serval, striped hyaena and aardwolf. For instance, striped hyaena have been recorded to move mostly cross-country rather than along roads in the Serengeti [12]. Similarly, mesocarnivores such as serval and aardwolf may avoid areas commonly used by apex predators, which would lower their capture rate along roads [70]. Future work could derive camera trap positioning from direct sightings or spoor, to prioritise locations where these species are likely to have better detectability.

The higher population density estimated for serval in miombo woodland indicates that this is an important habitat for the species in the region. One of the most extensive ecosystems in Sub-Saharan Africa, miombo woodlands cover a substantial portion of Tanzania's protected and unprotected land [71]. Miombo plays a key role in the livelihood of rural communities but faces unsustainable resource exploitation [72,73]. As such, increased woodland degradation and deforestation would negatively impact serval as well as a range of other mammal species. As miombo woodlands have received little conservation attention compared to *Acacia* habitats in East Africa [71], we recommend additional survey work across their extent to improve the understanding of these systems and protect their unique biodiversity.

370   Additionally, our results highlight the importance of the community-managed MBOMIPA
371   WMA for the striped hyaena and aardwolf in the Ruaha-Rungwa landscape. Along with the
372   adjacent RNP, MBOMIPA WMA provides the two hyaenids with suitable habitat at the edge
373   of their global range. More generally, the MBOMIPA WMA acts as a buffer zone between the
374   highly protected RNP and the surrounding villages, and our results demonstrate the potential
375   of community conservation in complementing more traditional conservation strategies,
376   particularly in areas with lower densities of vulnerable species such as striped hyaena.
377   Nevertheless, the camera trap survey found evidence of bushmeat hunting in the WMA;
378   although pictures show that hyaenas can break free from snares and survive with amputated
379   limbs, snaring and other non-selective poaching methods generally induce an increase in
380   anthropogenic mortality of non-target species in savannah ecosystems [74,75]. Considering
381   the species' low density in the Ruaha-Rungwa landscape, a conservation priority for striped
382   hyaena should be to reduce the impact of snaring on resident populations and assess the
383   corresponding risk to their viability.

384   In conclusion, our study gives an example of how data from camera trap surveys
385   targeting charismatic large carnivores can shed light on populations of lesser-known
386   carnivores, broadening the scope of capture-recapture studies beyond focal species. While
387   adjustments to sample design can help to extend the range of accessible species in surveys
388   [26], in this case, we were able to generate useful data without such adjustments. Similar
389   efforts, employing bycatch data, could be easily replicated elsewhere to provide information
390   on the spatial and population ecology of a range of species. Finally, we recommend
391   complementing the baseline estimates provided for serval, striped hyaena and aardwolf in the
392   Ruaha-Rungwa landscape with investigations into spatial variation in site use across the
393   landscape to determine the environmental and anthropogenic factors driving their habitat
394   selection.

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632   # Supporting information

633   **S1 Appendix. Example of individual identification.**

634   **S2 Appendix. Capture histories.**

635   **S3 Appendix. Trap layouts.**

636   **S4 Appendix. Survey grid summary information.**

637   **S5 Appendix. SECR model ranking.**