

High carnivore population density highlights the conservation value of industrialised sites

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Acknowledgements

We would like to thank Secunda Synfuels Operations Division of Sasol South Africa (Pty) Ltd. for supporting this research, the Faculty of Natural and Agricultural Science, University of the Free State, and the Wildlife Resource Association (WRA).

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41 **1. Abstract**

42 As the environment becomes increasingly altered by human development, the importance of
43 understanding the ways in which wildlife interact with modified landscapes is becoming clear.
44 Areas such as industrial sites are sometimes presumed to have little conservation value, but many
45 of these sites have areas of less disturbed habitats around their core infrastructure, which could
46 provide ideal conditions to support species such as mesocarnivores. We conducted the first
47 assessments of the density of serval (*Leptailurus serval*) at the Secunda Synfuels Operations
48 plant, South Africa. We ran three camera trap surveys to estimate serval density using a spatially
49 explicit capture recapture framework. Servals occurred at densities of 62.33-111.55 animals per
50 100 km², which are the highest recorded densities for this species. Our findings highlight the
51 significant conservation potential of industrialised sites, and we suggest that such sites could help
52 contribute towards meeting conservation goals.

53 **2. Keywords**

54 anthropocene, abundance, carnivore, felidae, private land

55 **3. Introduction**

56 Over the last centuries, there have been rapid and intense environmental changes caused by
57 increasing human numbers, technological advances and industrialisation (United Nations
58 Environment Programme 2012). Human alterations on the environments have resulted in a
59 decline in biodiversity, and are elevating extinction rates of species at a global scale (Chapin et
60 al. 2000). Currently more than 75% of the terrestrial surface is impacted by humans (Ellis et al.
61 2010; Ellis et al. 2013). These human activities are affecting biodiversity and ecosystems on
62 various scales as well as modifying existing ecosystems, creating unique urban environments
63 (Williams et al. 2009; Barbosa et al. 2010). In many cases biodiversity can be positively related

64 to human population at a regional scale due, for instance, to an enhanced spatial heterogeneity
65 between rural and urban environments, and the introduction of exotic species (McKinney 2002;
66 Sax and Gaines 2003). The influence of these modifications depends on both the scale and the
67 organisms involved (Barbosa et al. 2010).

68 Even within the most densely populated and intensively used areas, including urban landscapes,
69 humans rarely utilise all land, and tend to retain significant green or unused areas. These “green
70 spaces” hold ecological potential, and can reduce biodiversity loss by managing habitats to
71 support endangered species (Jackson et al. 2014), although further research is necessary to
72 understand the impacts of these processes (Northrup and Wittemyer 2013).

73 One species that that could be impacted by development is the serval (*Leptailurus serval*). The
74 serval is a medium-sized carnivore that feeds primarily on rodents (Ramesh and Downs 2015),
75 and is dependent on wetland habitats (Ramesh and Downs 2015/2) that are being rapidly lost
76 globally (Dixon et al. 2016). The species is listed as Least Concern on the global IUCN Red List
77 of threatened species (Thiel 2015), but is considered Near Threatened in South Africa
78 (Friedmann and Daly 2004). Serval have declined throughout their range (Ramesh and Downs
79 2013), and the principal threats to the species are loss and degradation of their wetland habitat
80 (Thiel 2011), trade of their skins (Kingdon and Hoffmann 2012), and persecution in response to
81 perceived predation of poultry (Henley 1997), although they only rarely prey on livestock (Thiel
82 2015). Data on population density and structure are critical to planning wildlife management and
83 implementing conservation initiatives (Barrows et al. 2005), but there have been few studies on
84 serval ecology, and conservation initiatives are hindered by poor knowledge of abundance
85 (Ramesh and Downs 2013).

86 In this study, we firstly aimed to estimate the population density of servals at the Secunda
87 Synfuels Operations plant, an industrial site in Mpumalanga province, South Africa, that
88 includes natural wetland within its boundaries (Fig. 1). We also aimed to assess the structure of
89 this serval population, in order to make inferences about population dynamics.



90 Fig. 1. Camera trap image of a serval at the heavily industrialised Secunda Synfuels Operations
91 plant in South Africa, recorded by Reconyx Hyperfire HC600 camera.

92 **4. Materials and Methods**

93 **3.1. Ethics statement**

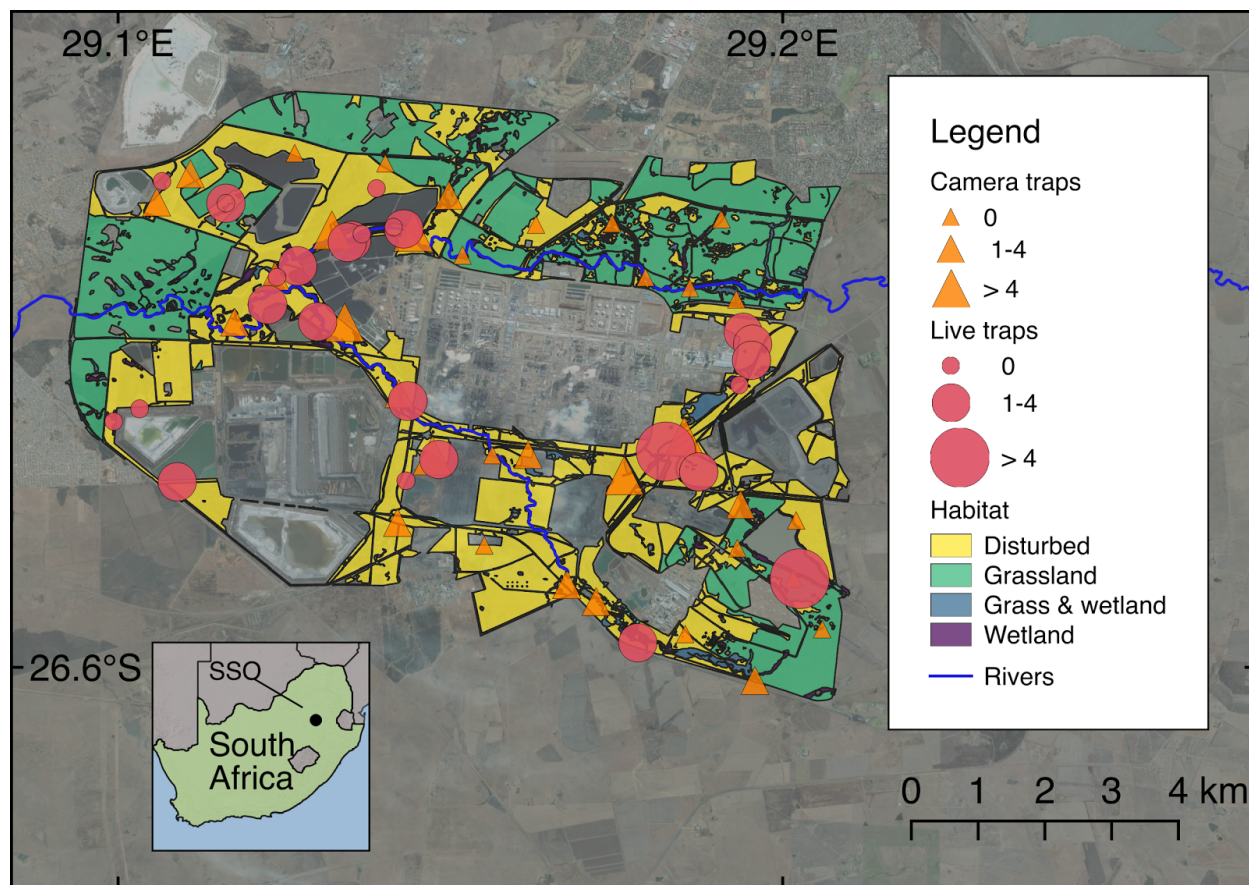
94 This project is registered at the Animal Care and Use Committee of the University of Pretoria
95 (Ethical clearance number: EC040-14) and the Mpumalanga Tourism and Parks Agency (Permit
96 number: 5467).

97 **3.2. Study Area**

98 The Secunda Synfuels Operations > Div of Sasol South Africa (PTY) Ltd, plant is located in
99 Secunda, Mpumalanga province, South Africa (Fig. 2), and it consists of a primary area (a
100 petrochemical plant) and a secondary area (which is made up of surrounding natural and

101 disturbed vegetation). The secondary area (hereafter referred to as the SSO) covers an area of 50
102 km² (central coordinates 26°31'45.62" S, 29°10'31.55" E). The secondary area is a gently to
103 moderately undulating landscape on the Highveld plateau, supporting short to medium-high,
104 dense, tufted grasses at different levels of disturbance. In places, small scattered wetlands (both
105 man-made and natural), narrow stream alluvia, and occasional ridges or rocky outcrops interrupt
106 the continuous grassland cover. Much of the study site (38%) is classified as relatively
107 untransformed habitat, which is managed in accordance to Secunda Synfuels Operations
108 Biodiversity Management Plan, to conserve the natural areas from degradation and improve the
109 ecological functionality of the disturbed land. The vegetation type is classified as Soweto
110 Highveld Grassland (Rutherford et al. 2006), and the area falls into the Grassveld Biome
111 (Mucina and Rutherford 2006). We used satellite images (Google 2014) to digitise the
112 boundaries of four major habitat types (Disturbed, Grassland, Grass & wetland, and Wetland),
113 which we used as site covariates in subsequent analyses.

114 The relatively unspoiled grassland represents the best form of Soweto Highveld Grassland on
115 site. The characteristic species include *Cymbopogon pospischilii*, *Pollichia campestris*,
116 *Walafrida densiflora*, *Eragrostis chloromelas*, *Gomphrena celosioides*, *Craibia affinis* and
117 *Cineraria cf. savifraga* (Matthews 2016). The grassland habitat has a low basal cover due to
118 grazing and during the rainy season the grass phytomass averages around 3-4 tons per hectare
119 (de Wet 2016). The grass and wetland habitat occurs mostly within the transition zones or dry
120 floodplains not typical of either wetland habitat or grassland habitat. These areas have a medium
121 cover, and include some species typical to wetlands. The wetland habitat is dominated by species
122 indicative of wetland zones and moist soils (Linström 2012). The phytomass here can be in
123 excess of 5 tonnes per hectare, and the growth is up to 1.5 meters above the ground level. The
124 disturbed habitat is dominated by weedy forbs with medium to very high density. The impact of
125 the weedy forbs is a thicket of basal cover on the surface and up to 1.5 meters above ground
126 level.



127 Fig. 2. Map showing the locations of camera traps and live traps at the Secunda Synfuels
128 Operations plant in South Africa. The size of points representing camera traps and live traps
129 diameter is proportional to the number of individual serval captured. Major habitat types are also
130 shown, along with satellite images illustrating the human-modified landscapes. Wetland and
131 Grass & wetland habitat types are difficult to visualise at this scale as they occur in very close
132 proximity to rivers.

133 3.3. Camera trapping

134 The study was underpinned by spatially explicit capture-recapture (SECR) framework. We
135 established an array of Reconyx Hyperfire HC600 camera traps at 34 camera trap stations over
136 an area of 79.4 km² throughout the study site (Fig. 2). We separated camera traps with an average
137 of 1.2 km (maximum 2.1 km), which was based on the home range size of serval (Ramesh et al.

138 2015). The study area of 79.4 km² is approximately two to three times the maximum area of
139 serval home range (Bowland 1990). The camera trapping area is therefore adequate (greater than
140 the home range size of male serval) to allow for robust density estimates using SECR framework
141 (Tobler and Powell 2013).

142 We placed camera traps on game trails and roads to maximise the probability of photographing
143 servals, and to facilitate access for camera maintenance. We mounted camera traps on fence
144 posts, 50 cm above the ground and 1 to 2 m from the trail. Vegetation in front of the camera traps
145 was cleared to reduce the rate of false triggers of the motion detector.

146 We conducted three surveys from 2014 to 2015, with each survey running for 40 days (see Table
147 1 for dates). Camera traps were programmed to operate 24 hours per day, with a one minute
148 delay between detections. Camera trap positions were kept constant within each survey and
149 between surveys. We visited each camera trap on a weekly basis to download the images, change
150 batteries, and ensure the cameras remained in working order. Camera Base 1.4 (Tobler 2010) was
151 used to manage the images collected by the camera traps. We identified servals manually using
152 individual markings such as spot patterns and scars.

153 3.4. Live trapping

154 Live trapping formed part of a larger study investigating serval spatial and disease ecology. We
155 used the live trapping data to record the capture rate and population structure of the serval
156 population at the study site to validate our camera trapping study. Serval were trapped using 16
157 steel trap cages measuring 200 cm x 80 cm x 80 cm, deployed at 29 trap sites throughout the
158 study site. Traps were baited with helmeted guineafowl (*Numida meleagris*) for a total of 287
159 trap nights between 2014 and 2017. Servals were immobilised by a veterinarian using one of the
160 following drug combinations: 1) KBM-5: ketamine (5.0 mg kg⁻¹), butorphanol (0.2 mg kg⁻¹), and
161 medetomidine (0.08 mg kg⁻¹); 2) KBM-8: ketamine (8.0 mg kg⁻¹), butorphanol (0.2 mg kg⁻¹), and
162 medetomidine (0.08 mg kg⁻¹); 3) ZM: zoletil (5.0 mg kg⁻¹) and medetomidine (0.065 mg kg⁻¹); 4)
163 AM: alfaxalone (0.5 mg kg⁻¹) and medetomidine (0.05 mg kg⁻¹); or 5) ABM: alfaxalone (2.0 mg

164 kg⁻¹), butorphanol (0.2 mg kg⁻¹), and medetomidine (0.08 mg kg⁻¹) ([Blignaut et al. in review](#)).
165 Drugs were administered intramuscularly using a blowpipe. If serval showed signs of inadequate
166 drug dosages, they were topped-up with the same combinations. Where administered,
167 medetomidine and butorphanol were pharmacologically antagonised with atipamezole (5 mg
168 mg⁻¹ medetomidine) and naltrexone (2 mg mg⁻¹ butorphanol), respectively. After examination,
169 animals were released at the same site where they were captured.

170 Animals with a mass of 3-8 kg were considered to be juveniles (up to approximately six months
171 old, to the stage where the canines are developed). Servals with a mass of 8-11 kg were
172 categorised as sub-adults (6-12 months old, just before they are sexually mature). Animals 11-15
173 kg (approximately 12 to 18 months and older) were considered to be adults (Sunquist and
174 Sunquist 2002).

175 3.5. Data analysis

176 We estimated serval density by fitting likelihood based SECR (Efford 2004) models to camera
177 trap data using the package secr (Efford 2017) in R version 3.4.3 (R Development Core Team
178 2017). The advantage of SECR models over traditional density estimation methods is that they
179 do not require the use of subjective effective trapping areas, and instead estimate density directly
180 (Tobler and Powell 2013). This is achieved by estimating the potential animal activity centres in
181 a predefined area using spatial location data from the camera traps (Efford 2004). The spacing of
182 the activity centres is related to the home range size of the animals, and as such the detection
183 probability of each animal is a function of the distance from the camera trap to the activity
184 centre. Detection is modelled using a spatial detection function which is governed by two
185 parameters; the encounter rate at the activity centre (detection probability; λ_0) and a scale
186 parameter (σ) which describes how the encounter rate declines with increased distance from the
187 activity centre (Efford 2004). We tested for three different spatial detection functions;
188 half-normal, hazard and exponential. We ranked models based on Akaike information criterion
189 (AIC), and found overwhelming support for the hazard rate spatial detection function (Table S1).

190 All subsequent models were fitted with the hazard rate detection function.

191 We fitted SECR models by maximising the full likelihood where the scale parameter was kept
192 constant, but we let the encounter rate vary by biologically plausible hypotheses. The scale
193 parameter is largely affected by home range size, and hence the sex of the animal (Sollmann et
194 al. 2011/3). However, we were unable to determine the sex of individual serval from the
195 photographs, and could therefore not model variation in the scale parameter. We first fitted a
196 model in which serval showed a behavioural response at λ_0 , as animals can become trap happy
197 or trap shy (Wegge et al. 2004). Secondly, we tested the effect of habitat on λ_0 , as serval prefer
198 wetlands (Bowland 1990), which would result in higher detections in these habitats. We captured
199 camera-specific habitat variables from the vegetation classification. Thirdly, we coded each year
200 and season as a separate session, and used the multi-session framework in `secr` to test the effect
201 of season on serval density, with constant λ_0 . We lastly fitted a model in which λ_0 varied with
202 both season and habitat type. These models were contrasted against a null model, in which all
203 variables were kept constant.

204 We used AIC to rank models, considering models with $\Delta\text{AIC} < 2$ to have equal support
205 (Burnham and Anderson 2004). The buffer width for analysis was set at 3,000 m, which resulted
206 in the inclusion of an informal housing settlement and a residential area in the state space buffer.
207 Since it is highly unlikely that serval will utilise these areas (as well as the primary industrial
208 area) we excluded these areas from the state space buffer (Fig. S1). All data and R code used for
209 analysis are available in (Loock et al. 2018).

210 **4. Results**

211 **4.1. Camera trapping**

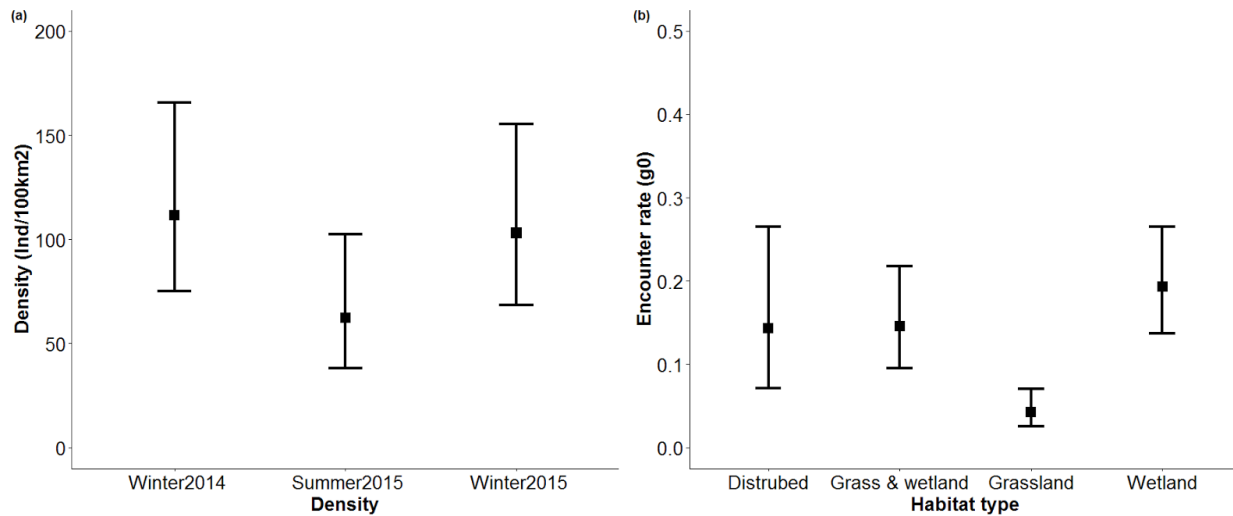
212 During a camera trapping effort of 3,590 trap days, we photographed a total 61 serval spanning
213 three separate sessions (Table 1). The number of individual serval captures did not differ greatly
214 between sessions, although the highest number was captured during the wet period of 2015

215 (Table S3, Fig. S2).

216 The two most parsimonious SECR models ($\Delta AIC < 2$) both indicated that the encounter rate (λ_0) was affected by habitat type (Table S4). There was also strong support that serval density is
217 session dependant ($\Delta AIC = 0.098$; $w = 0.487$; Table S3). To estimate serval density we therefore
218 fitted an SECR model with density dependent on session (a proxy for season and year
219 combination) and encounter rates dependent on habitat type. Serval population density estimates
220 at SSO varied from 62.33 (SE=16.03) to 111.55 (SE=22.76) animals per 100 km² (Fig. 3a).
221 Highest estimates were recorded during the dry seasons (Winter 2014: 111.55 [SE=22.76] &
222 Winter 2015: 103.06 [SE=21.76]) compared to the single summer season (Summer 2015: 62.33
223 [SE=160.3]; Fig. 3a). Vegetation type had a significant effect on serval encounter rates, where
224 grassland had the lowest encounter rate (0.04 [SE=0.01]) compared to wetlands with the highest
225 (0.19 [SE=0.03]; Fig. 3b).
226

227 Table 1. Details of serval camera trapping surveys conducted at SSO in Mpumalanga province,
228 South Africa, in 2014 and 2015.

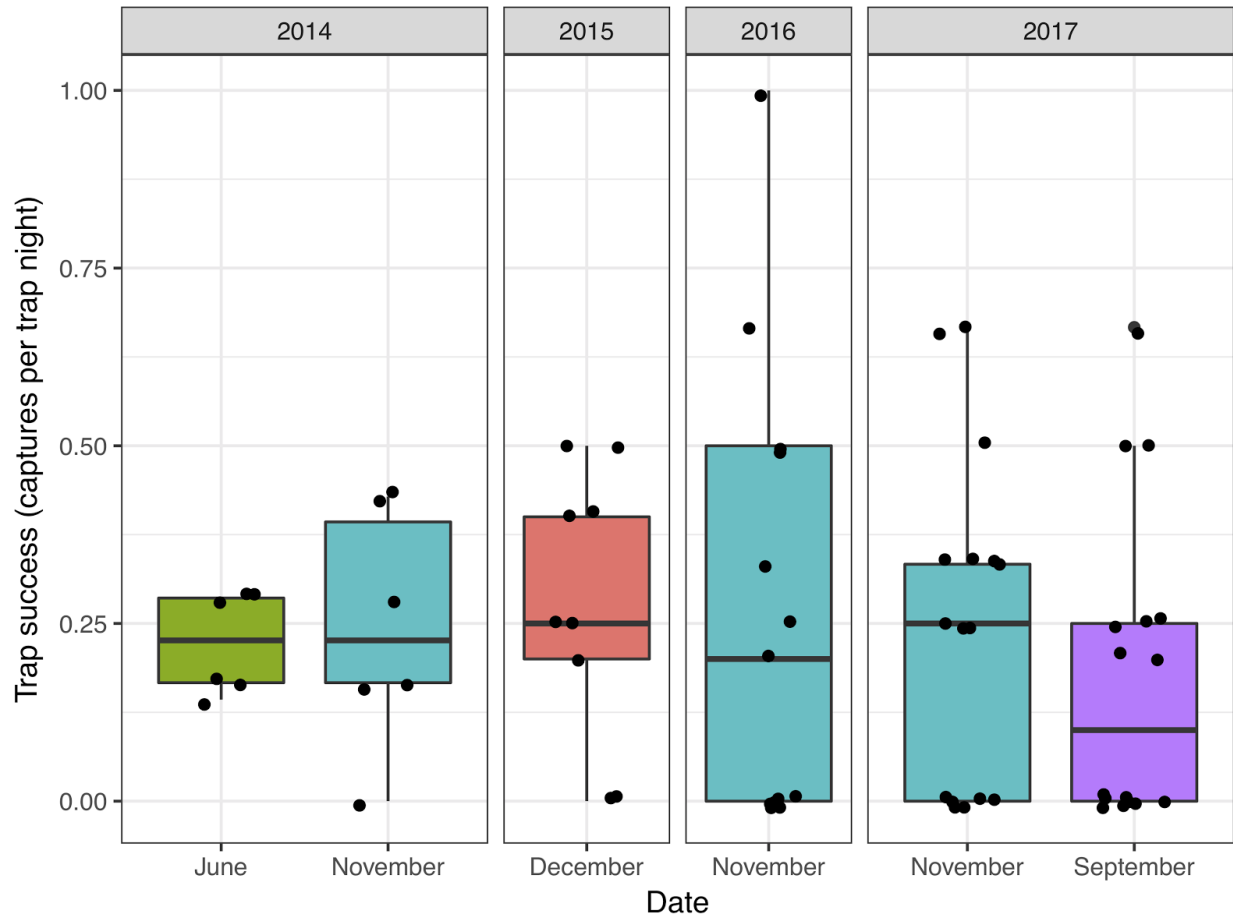
Survey	Starting date	End date	Camera trap nights	Survey area (km ²)	Number of serval photographic captures	Number of individual serval photographed
Winter 2014	2014/08/05	2014/09/14	1,105	79.4	332	22
Summer 2015	2015/02/21	2015/04/02	1,333	79.4	580	34
Winter 2015	2015/06/20	2015/07/30	1,152	79.4	672	31
<i>Total</i>			3,590	79.4	1,584	61



274 Fig. 3. Serval density estimates for each camera trap survey conducted at SSO indicating a)
275 influence of season on density, and b) effect of habitat type on serval encounter rate.

276 4.2. Live trapping

277 We captured 65 individuals, of which four were also recaptured on a second occasion. This
278 comprised of a total of 26 adult males, 19 adult females, 11 sub-adults, and seven juvenile
279 animals. This resulted in a mean trapping success rate of 0.21 captures per trap night (excluding
280 recaptures). Trapping success rate varied little between sessions (Fig. 4).



281 Fig. 4. Box plot showing trap success rate for serval captures at SSO from 2014 to 2017.

282 5. Discussion

283 5.1. Comparative serval density

284 In our three camera trap surveys at SSO, we estimated serval population density to be 111.55,
285 62.33, and 103.06 animals per 100 km², which are the highest densities recorded in the literature.
286 Although there are no data available for serval live trapping rates, rates of 0.0015-0.017 captures
287 per trap night are much more typical for other mesocarnivores such as jaguarundi (*Puma*
288 *yagouaroundi*), oncilla (*Leopardus tigrinus*), tayra (*Eira barbara*), and feral cat (*Felis silvestris*
289 *catus*) using cage traps (Molsher 2001; Michalski et al. 2007; McGregor, H W, Hampton J O,

290 Lisle, D, Legge, S 2016), which are an order of magnitude lower than serval live capture rates at
291 SSO (0.21 captures per trap night). Although great care must be taken when comparing trapping
292 rates between different locations and species, the live trap rates at SSO nevertheless appear to be
293 consistently very high, which supports the high population densities estimated using camera trap
294 data.

295 Our high estimates of serval densities at SSO contrast with more typical densities reported in
296 Luambe National Park in Zambia (9.9 animals per 100 km² (Thiel 2011), Bwindi Impenetrable
297 National Park in Uganda (9 animals per 100 km² (Andama (2000), cited in Kingdon and
298 Hoffmann 2012)), and on farmland in the Drakensberg Midlands, South Africa (6.5 animals per
299 100 km² (Ramesh and Downs 2013)). However, there is evidence that serval can attain such high
300 densities. For example, Geertsema (1985) reported a serval density of 41.66 animals per 100 km²
301 in the Ngorongoro Crater, Tanzania.

302 High population densities of other carnivore species have also been reported in human-modified
303 habitats such as urban areas. Coyotes (*Canis latrans*), raccoons (*Procyon lotor*), red foxes
304 (*Vulpes vulpes*), and Eurasian badgers (*Meles meles*), for example, all thrive in urban landscapes
305 (Bateman and Fleming 2012; Scott et al. 2014). Carnivore species able to adapt to urban
306 environments often succeed in these areas due to high food availability, favourable climatic
307 effects, and the reduced threat of intraguild predation because of the absence of larger apex
308 predators (Fuller et al. 2010). We provide several, not necessarily mutually exclusive theories, to
309 explain the high serval density we observed at SSO.

310 Firstly, servals in the SSO are protected from persecution. Such persecution can have large
311 effects on carnivore densities. For example leopards (*Panthera pardus*) in livestock/game
312 farming areas only attain around 20% of their potential density compared to protected areas free
313 from persecution (Balme et al. 2010). Servals outside protected areas are frequently persecuted
314 by livestock farmers (Henley 1997) as they are often mistakenly blamed for livestock predation
315 (Skinner and Chimimba 2005), but at SSO this is not the case, which could lead to higher
316 population densities (Cardillo et al. 2004). Secondly, servals are the largest remaining carnivore
317 species occurring at ecologically effective densities at SSO, so there is little interspecific

318 competition from larger carnivores. In other areas, the presence of other medium- and
319 large-bodied carnivores could otherwise limit serval population densities (through intraguild
320 predation), so their absence can lead to mesopredator release, such as through increased survival
321 of young (Ritchie and Johnson 2009). For example, the absence of large carnivores such as lions
322 (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) in northern South Africa is thought to
323 have led to the competitive release of cheetahs (*Acinonyx jubatus*) (Marnewick et al. 2007).
324 Thirdly, the abundance of disturbed habitat at SSO could also facilitate high serval population
325 density. Disturbed habitat can be highly productive (Williams et al. 2018), and provide shelter
326 and food resources for species such as rodents that serval prey upon (Taylor 2013), providing
327 abundant food and in turn supporting a high abundance of serval.

328 Although the population density of serval recorded at SSO was exceptionally high, the structure
329 of this serval population was similar to those at other sites. The number of adult males per 100
330 adult females captured in live traps at SSO was 137, which is within the range reported in the
331 literature (50-220 in KwaZulu-Natal ((Bowland 1990; Ramesh et al. 2016); 100 in the
332 Ngorongoro Crater, Tanzania (Geertsema 1985)). Similarly, the proportion of the population at
333 SSO that was comprised of juvenile and sub-adult individuals (0.69) was very similar to other
334 populations (0.64 in the Ngorongoro crater; (Geertsema 1985)). It therefore appears that although
335 the serval population density at SSO is very high, the structure of the population is not unusual,
336 which is not indicative of a rapidly declining or increasing population size (Harris et al. 2008),
337 supporting our findings that the serval population density at the study site appears to be relatively
338 stable.

339 Although servals appear to thrive in close proximity to such a heavily industrialised site, we
340 suggest that further research is conducted to identify any potential effects of industrial activity
341 (Raiter et al. 2014), such as the influence of noise and air pollution on the physiology and
342 behaviour of wildlife in the vicinity (Morris-Drake et al. 2017).

343 5.2. The impacts of modified landscapes

344 In recent years the expansion of infrastructure has progressed more rapidly than during any other
345 period in history (Laurance et al. 2015), and industrial sites such as mines and fossil fuel
346 processing plants are not the only developments that could have impacts on wildlife. The
347 growing road network, for example (Ibisch et al. 2016), has large direct and indirect ecological
348 impacts such as causing wildlife-vehicle collisions, polluting the environment, disrupting animal
349 migrations and gene flow, and providing access to invading species and humans, facilitating
350 further degradation (Laurance et al. 2009; Sloan et al. 2016). The rapidly growing number of
351 hydroelectric dams (Zarfl et al. 2014) increases the risk of habitat fragmentation through
352 deforestation, in addition to disrupting freshwater ecosystems (Finer and Jenkins 2012).
353 Similarly, the development of urban and agricultural areas fragments and destroys habitats
354 (Ripple et al. 2014). Consequently, delineating how the changing environment affects
355 biodiversity will be an increasingly important theme of future research.

356 But not all the impacts of anthropogenic development on wildlife are negative. The high serval
357 densities at SSO are remarkable as the site is very heavily industrialised. Nature reserves and
358 exclusion zones surrounding industrialised areas such as SSO have the potential to balance
359 resource utilisation with biodiversity conservation (Edwards et al. 2014). Some industrial
360 installations such as mines have created nature reserves, which can benefit biodiversity
361 conservation. The Mbalam iron ore mine in Cameroon has set aside land to protect rare forest
362 mammals (Edwards et al. 2014). Private nature reserves created around the Venetia diamond
363 mine in South Africa and the Jwaneng diamond mine in Botswana support a broad complement
364 of large mammals including elephants (*Loxodonta africana*), lions (*Panthera leo*), leopards
365 (*Panthera pardus*), cheetahs, African wild dogs (*Lycaon pictus*), brown hyaenas (*Hyaena*
366 *brunnea*), and black-backed jackals (*Canis mesomelas*) (Smallie and O'connor 2000; Kamler et
367 al. 2007; Houser et al. 2009; Jackson et al. 2014). The Sperrgebiet exclusion zone in Namibia,
368 established to protect diamond deposits (Edwards et al. 2014), has now been proclaimed a
369 National Park (Wiesel 2010). The consequent changes in the ecological functions of these human
370 modified areas can produce a new combination of species, sometimes modifying and, in many

371 cases, increasing the local richness (Hobbs et al. 2006; Pautasso et al. 2011).
372 Studies such as this highlight the complexity of the relationship between wildlife and the
373 human-modified environment, and suggest that the potential conservation value of industrialised
374 sites should not be overlooked. This underscores the importance of sound ecological
375 management in these areas. Such sites could be incorporated into wildlife management plans,
376 and could help to achieve goals such as the conservation of threatened species. This could be
377 achieved, for example, through the formation of partnerships between industry and the non-profit
378 sector or governmental agencies, such as the partnership between Eskom and the Endangered
379 Wildlife Trust (EWT) to reduce the threats posed by electricity infrastructure to wildlife in South
380 Africa (Jenkins et al. 2010).

381 **6. Conclusion**

382 Servals occur at much greater densities at SSO than have been recorded elsewhere. Capture rates
383 on both camera traps and live traps were remarkably high. High densities may be due to
384 favourable conditions such as a high abundance of rodent prey and the absence of persecution or
385 competitor species. Despite the highly industrialised nature of the site, serval population
386 structure appears to be similar to other natural sites. We suggest that the potential value of
387 industrial sites, where they include areas of relatively natural habitats, may be underappreciated
388 by conservationists, and that these sites could help meet conservation objectives.

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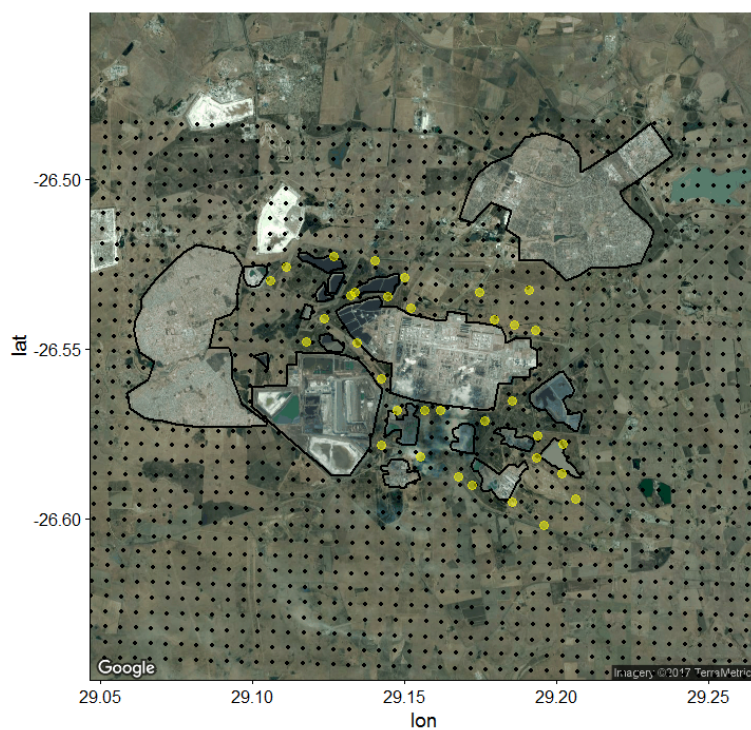
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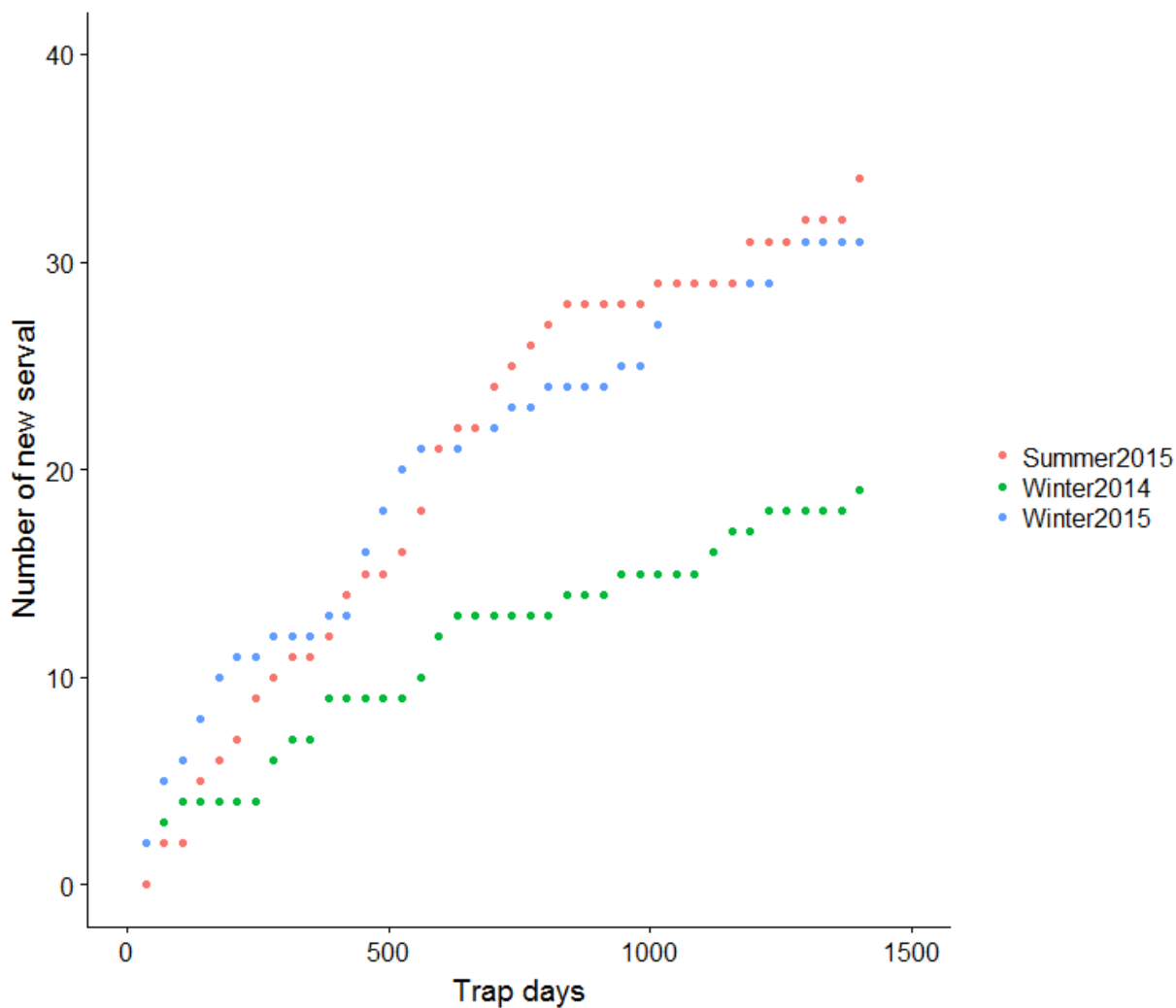
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565 **Supplementary information**

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567 Fig. S1. Map showing the locations of camera traps (yellow points) and the state space (black
568 points), illustrating the areas excluded from the state space at SSOP in South Africa.



569 Fig. S2. Cumulative frequency curve showing the relationship between the cumulative number of
570 individual serval identified on the camera traps at SSO in South Africa.

571 Table S3. Model results showing the seasonal effect on serval density at SSO.

	Density (individuals per 100 km²)	Standard error	Lower confidence limit	Upper confidence limit
Winter 2014	111.54	22.76	75.07	165.72
Winter 2015	103.06	21.76	68.44	155.19
Summer 2015	62.33	16.02	37.96	102.35

Table S4. Model results showing the habitat effect on detection probability (g0). Model name: a) (Mhab.sec) models the detection probability (g0) on habitat type. b) (Mdens.habitat) models the how density is affected by season and year and account for habitat in detection probability c) (Mb.sec) models the learned response to detection d) (Mseason) models density affected by season and year. e) (m0.sec) the Null model.

Model name	Model specification	Detection Function (detectfn)	Number of parameters (npar)	Log-Likelihood (logLik)	Akaike Information Criterion(AIC)	Corrected AIC (AICc)	Difference in Corrected AIC (dAICc)	AICc model weight (AICcwt)
Mhab.sec	D~1 g0~Habitat sigma~1 z~1	hazard rate	7	-1015.43	2044.854	2046.327	0	0.5122
Mdens.habitat	D~session g0~Habitat sigma~1 z~1	hazard rate	9	-1013	2043.993	2046.425	0.098	0.4878
Mb.sec	D~1 g0~b sigma~1 z~1	hazard rate	5	-1028.51	2067.03	2067.799	21.472	0
Mseason	D~session g0~1 sigma~1 z~1	hazard rate	6	-1030.09	2072.179	2073.269	26.942	0
M0.sec	D~1 g0~1 sigma~1 z~1	hazard rate	4	-1033.59	2075.185	2075.692	29.365	0