From big spots to little spots: Influence of camera trap deployment on spatial capture-recapture estimates of servals (*Leptailurus serval*) in Ithala Game Reserve

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Plagiarism declaration

I know that plagiarism is wrong. Plagiarism is using another's work and to pretend that it is one's own.

I have used the journal *Conservation Biology* format as the convention for citation and referencing. Each significant contribution to, and quotation in, this project from the work or works of other people has been attributed, cited, and referenced.

This project is my own work. I have not allowed, and will not allow, anyone to copy my work with the intention of passing it off as his or her own work.

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Abstract

Servals (*Leptailurus serval*) face a range of threats which can impact their populations, but we have little information on their conservation status across much of their range. Repeated population density estimates are the most useful parameter for assessing population trends and the impacts of anthropogenic changes (e.g. habitat loss and poaching) on serval densities. These could further be used to establish a correlation between any changes in this population and relevant highlighted anthropogenic influences that may exist with relevance to their conservation vulnerability. However, such surveys for small cryptic carnivores are rare, largely because funding and hence research is heavily biased towards large, charismatic and threatened species. Fortunately, servals and other mesocarnivores are frequently recorded as by-catch in camera trap surveys designed for larger carnivores which offers a unique opportunity to explore the viability of using these 'bi-catch' data for the determination of population estimates of cryptic carnivores. Spatial capture-recapture models are the most robust means of estimating the densities of individually identifiable species like servals. In this study, I investigate whether the ongoing leopard (Panthera pardus) surveys in Ithala Game Reserve can be used to accurately estimate serval density and thus provide the first long term assessment of serval population trend within a protected area in South Africa.

To achieve this, I designed a camera trap array to estimate serval density specifically (i.e. smaller intertrap distances and the inclusion of wetland habitat) and ran it simultaneously with a less intensive survey designed to estimate leopard population density in Ithala. The leopard array produced an estimate of 1.73 ± 0.80 (0.76-3.97) servals/100 km^2 compared to an estimate of 2.49 ± 0.81 (1.24-4.63) servals/100 km^2 from the serval array. In line with standard analysis of the results, the approximately 75% overlap in the 95% confidence intervals suggests the two density estimates are comparable. The inclusion of vehicle traffic (as a measure of anthropogenic disturbance) and vegetation (as a proxy for habitat suitability) as covariates did not improve the serval specific density estimate.

Based on these findings I proceeded to use the long-term leopard survey data to produce annual density estimates for serval over a seven-year period (2013-2019). Serval density has decreased from the high of 9.66 (± 2.1) servals/100 km2 recorded in 2014 to a low of 1.42 (± 0.6) in 2018. A similar decline was evident in the leopard density estimates, suggesting that both these two carnivore species are facing some form influence that is threatening their population numbers in Ithala. Recent social surveys in nearby neighbouring communities reveal that snaring and hunting with dogs are both common methods of illegal hunting and such activities may be greatly facilitated in the northern section of Ithala owing the absence of a boundary fence.

This study suggests that serval density can be reliably estimated using data collected as part of ongoing leopard surveys in protected areas throughout South Africa. Given the paucity of such data the approach used in this study should be expanded to provide a more comprehensive assessment of serval population status and the generality of the finding that serval density is declining within a protected area previously considered to be a stronghold for this species.

1. Introduction

Large mammalian carnivores are ecologically important because of their impacts on ecosystem dynamics through trophic interactions (Estes et al. 2011; Ripple et al. 2014; Satterfield et al. 2017). Despite this, large carnivores have experienced substantial population declines and historical range reduction globally (Ray et al. 2005; Ripple et al. 2014) with numerous site extinctions throughout western and central Africa (Brugière et al. 2015). These declines are largely due to habitat fragmentation, prey depletion and direct persecution (Brassine and Parker 2015). Removal of apex carnivores has a disruptive influence on ecosystem structure and function (Estes et al. 2011; Ripple et al. 2014; Satterfield et al. 2017; Tambling et al. 2018) and consequently large carnivores have often been used as critical indicators of broad-scale conservation status (Soulé and Terborgh 1999). Monitoring carnivore populations is a critical ecological parameter for informing conservation decisions, as well as effective ecological management (Obbard et al. 2010; Nichols 2014). Estimates of density, population numbers, survival, recruitment and spatial distributions are critical to plan, implement and evaluate conservation interventions (Polisar et al. 2014; Karanth et al. 2017) as well as assess ecosystem stability and health.

In southern Africa the majority of carnivore research and funding has focused on a handful of large, charismatic carnivores (Caro 2003; Ogada et al. 2003; Ray et al. 2005; Dalerum et al. 2008; Snyman et al. 2015) despite medium and small carnivores having higher relative species richness per area (Ray et al. 2005; Roemer et al. 2009; Tambling et al. 2018). When assessing felid research funding specifically, more than 98% of global donations for felid conservation efforts have been dedicated to the seven larger cat species, leaving less than 2% of funding available for the other 33 smaller cat species. (J. Sanderson, pers. comms, see Figure 1).

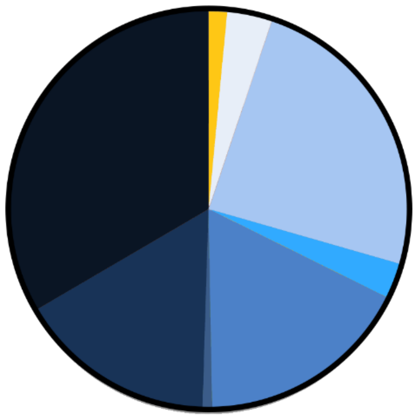

Figure 1. Percentage of donations given towards wild cat conservation according to species. Data provided by the Small Cat Conservation Fund (Jim Sanderson, pers. comm.).

Apex predators supress mesocarnivore abundance through direct competition and predation (Wang et al. 2015; Pretorius 2019) and with the removal of apex predators, mesocarnivores may assume the role of apex predators (Ripple et al. 2014) making them vital for ecosystem functioning and biodiversity in disturbed habitats (Tambling et al. 2018). Most recent research on mesocarnivores has focussed on their management as a threat to livestock (Roemer et al. 2009; Kerley et al. 2018). However, mesocarnivores also play an important role in regulating ecosystems and are often drivers of ecosystem function, structure and dynamics (Roemer et al. 2009; Tambling et al. 2018; Williams et al. 2018). In natural ecosystems, predators will exert top-down regulatory pressure on prey and hence their absence results in deleterious ecological cascades, including the loss of plant diversity, biomass and productivity (O'Bryan et al. 2018). Carnivores are thus often considered flagship or keystone species in many systems and more recently, sentinels of ecosystem health (O'Bryan et al. 2018). Mesocarnivores specifically provide important ecosystem services through small mammal population offtake (Ramnanan et al. 2016), seed dispersal (Silverstein 2005) and waste removal when scavenging (Ćirović et al. 2016).

Despite the precarious conservation status of some species and their ecological importance, research on mesocarnivores remains limited (Martinoli et al. 2006; Satterfield et al. 2017). A recent study by Pretorius (2019) revealed that mesopredator occupancy within protected areas of KwaZulu-Natal was low and was higher in more disturbed reserves. Occupancy was also higher in neighbouring farmland than reported for reserves (Ramesh and Downs 2015a; Ramesh et al. 2017) suggesting that mesopredator numbers are suppressed within protected areas with an intact large predator guild. The serval (*Leptailurus serval*) is an example of a mesocarnivore for which we have limited information within protected areas of South Africa with most research to date having been conducted on farmland (Ramesh and Downs 2013) and disturbed areas including industrial nodes (Loock et al. 2018). Servals, like many other species, face habitat loss and fragmentation (Ramesh and Downs 2013), however, some studies show that this may not necessarily be to the detriment of serval population, depending on the level and intensity of the degradation and resulting habitat (Loock et al. 2018). They are also persecuted for their skins, which are used for 'muti' (traditional African medicinal use) and in the illegal fur trade (Ramesh et al. 2016a; Manqele et al. 2018), killed in retaliation for poultry predation (Thiel 2015; Manqele et al. 2018) and are often victims of poisoning targeting other species such as black backed jackal (*Canis mesomelas*) and caracal (*Carcal caracal*) (Ramesh et al. 2016a). Understanding serval density across time and space and filling a much-needed knowledge gap on their populations within protected areas in South Africa is essential to their conservation and management.

Description and Ecology

The serval is a medium sized felid, with males ranging in size from 7.9-18.0 kg and females from 6.0-12.5 kg (Hunter 2018). Servals boast the longest legs of any cat relative to body length. Long legs and an elongated neck give the serval a height advantage when hunting in long grass. The coat is yellowish-buff and dappled with bold spots that coalesce into blotches on the limbs, tail and neck (Figure 2). A paler, buff-coloured morph with faint freckled spots has been described as the 'servaline' morph and occurs in West and Central Africa (Hunter 2018). Melanistic individuals have also been recorded in Equatorial highlands and forest-savanna ecotone (Hunter 2018).

Figure 2. An adult serval showing the large ears, long legs and solid spot pattern photographed by Johan Van Zyl.

Servals are typically crepuscular and/or nocturnal (Geertsema 1985; Thiel 2011; Ramesh and Downs 2013), but may be active during the day when lactating (females) (Geertsema 1985) or living in areas with a high density of larger predators (Bohm and Hofer 2018). Servals are solitary and generally territorial, although same-sex adults appear relatively tolerant of each other and home ranges overlap considerably (Geertsema 1985; Hunter 2018). Breeding season varies, with peak births occurring in the warm summer months of November to March in Southern Africa and August to November in the Ngorongoro Crater (Hunter 2018). Kittens are born in abandoned burrows, rock cavities or under a thicket after a gestation period of approximately 73 days (range 70-79 days, n=15) (Stuart and Wilson 1988; Thiel 2011; Hunter 2018). Litters average two to three kittens, although up to six have been recorded (Smithers 1978). Kittens are dependent on their mothers until six to eight months of age (Hunter 2018), but typically remain with their mothers for a full year (Bowland 1990). Lions (*Panthera leo*), leopards (*Panthera pardus*), crocodile (*Crocodylus niloticus*) and domestic dogs (*Canis familiaris*) are known predators of servals and martial eagles (*Polemaetus bellicosus*) have been recorded preying on kittens. Longevity in the wild is around 11 years and in captivity up to 23 years of age (Thiel 2011; Hunter 2018).

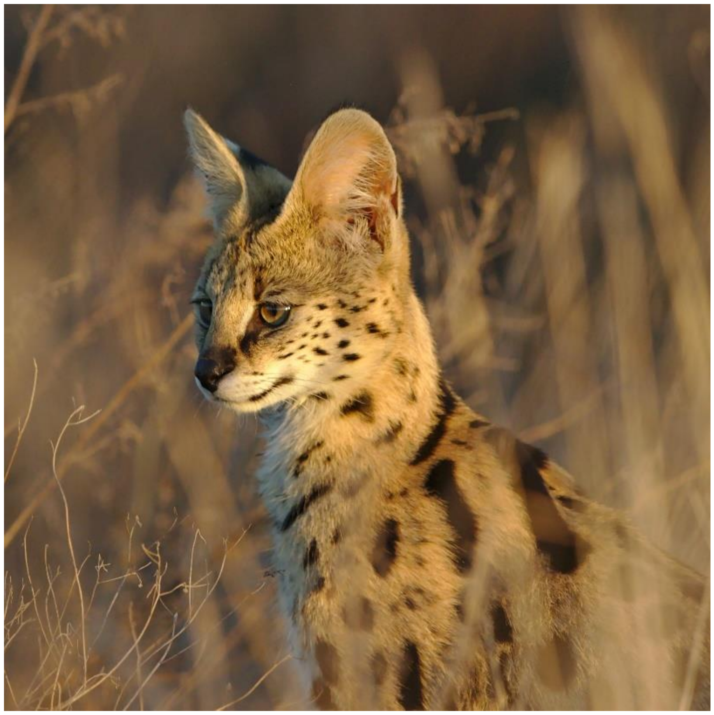

Figure 3. Serval showing the variation in coat patterns from spots transitioning into blotches along the neck photographed at Marievale Bird Sanctuary, Gauteng, South Africa by Derek Keats.

Distribution

Serval are cryptic felids occurring throughout much of sub-Saharan Africa (Thiel 2015, see Figure 4). These cats are considered to be grassland and savannah wetland specialists, feeding mostly on the small mammals that are abundant in these habitats (Geertsema 1985; Bowland and Perrin 1993; Thiel 2011; Ramesh and Downs 2015a; Edwards et al. 2018). Tracking the movement of individuals revealed that servals spend more time in wetland and riverine habitats than in open grasslands and croplands (van Aarde and Skinner 1986; Perrin 2001; Ramesh and Downs 2015a). Despite a broad distribution range, being habitat specialists most likely restricts them to smaller areas at a local scale (Ramesh et al. 2016a).

In southern Africa, servals are found throughout Mozambique, Zambia and Zimbabwe, as well as near the Okavango Delta in Botswana and in north-east Namibia (Bowland 1990). Within South Africa, servals have been historically recorded in the Free State (Hunter and Bowland 2013), North West, Limpopo, Mpumalanga, KwaZulu-Natal, and Eastern Cape provinces (Skead 2011; Ramesh et al. 2016a). Servals were historically reported as occurring along the coastal and sub-coastal belt of the Eastern Cape but were thought to have been extirpated from the province in 1987 (Bowland 1990; Skead 2007). Servals were reintroduced in the early 2000s to Kwandwe and Shamwari Private Game reserves (Hayward et al. 2007) and have been recorded on other reserves and properties in the province in recent years (Herrmann et al. 2008; Ramesh et al. 2016a). In 2011, Thorn et al. estimated a 37% increase in serval range since 2000 in North West province. Ramesh et al. (2016) have also recently recorded servals in the Western Cape. Servals have been observed at properties and reserves in Gauteng in recent years and have been captured on camera traps at Rietvlei Nature Reserve (N. Keen, Rietvlei Nature Reserve, pers. comm.) and by photographers in Marievale Bird Sanctuary (see Figure 3). Range expansion in South Africa has been reported (Herrmann et al. 2008; Ramesh et al. 2016a; Power et al. 2019) which may be attributed to the creation of artificial wetlands by means of irrigation systems and dams for agricultural use (Herrmann et al. 2008; Loock et al. 2018).

The only published abundance estimates for servals in South Africa are from a study in the KwaZulu-Natal midlands (Ramesh and Downs 2013) and an industrial site in Mpumalanga (Loock et al. 2018). Serval distribution and population status within South Africa is thus relatively unknown, which impedes effective conservation management of the species.

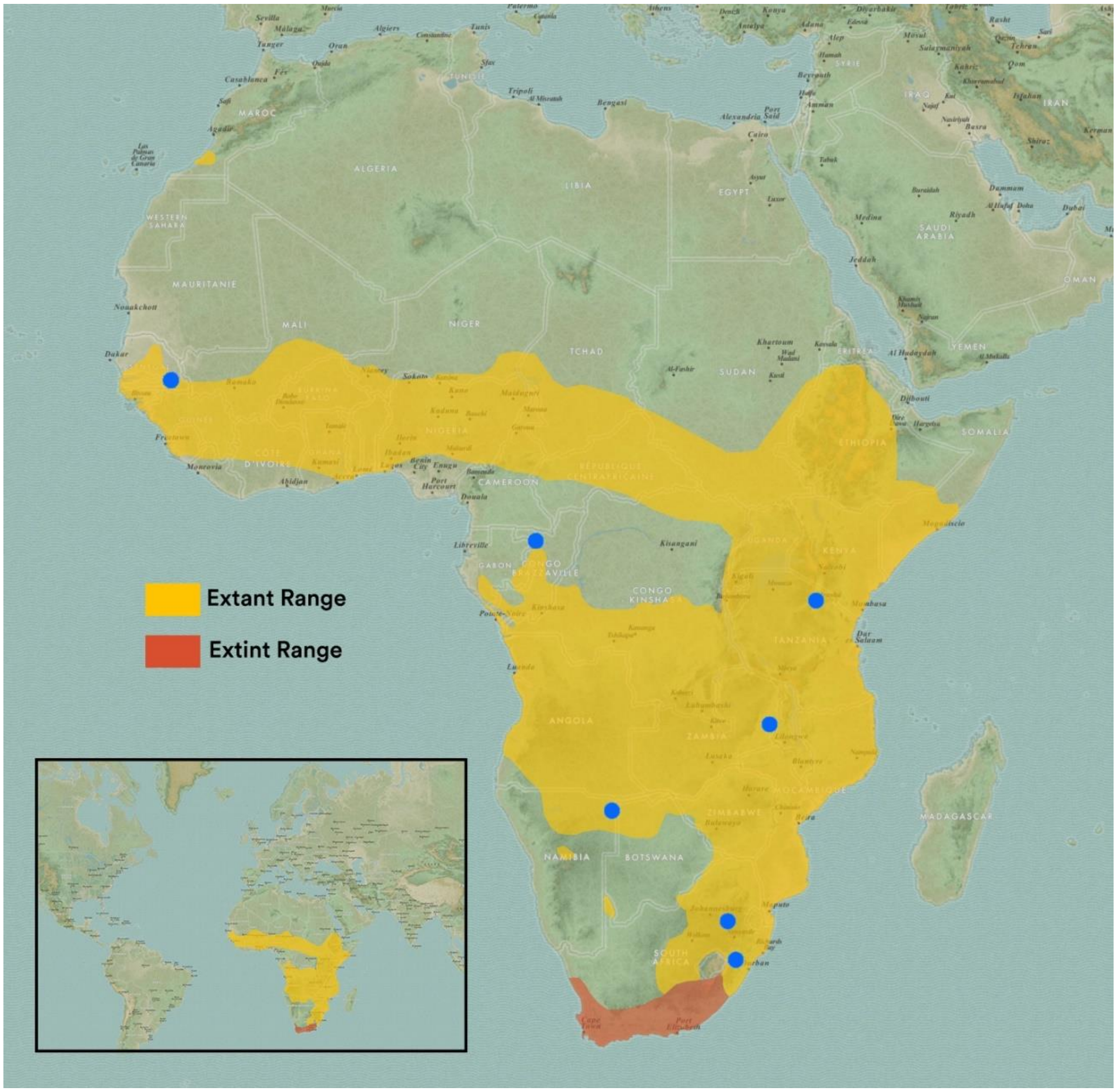

Figure 4: Serval distribution map created from the serval extant range (yellow) and serval extinct range (red) (IUCN 2015). Blue dots indicate locations of published serval density estimates.

Diet

Servals specialise in hunting small mammals, with a high portion (80.0-93.5%) of their diet comprising of rodents (Bowland and Perrin 1993; Ramesh and Downs 2015b; Thiel 2015; Hunter 2018). A scat analysis by Ramesh and Downs (2015b) found that the bulk of serval diet (57.8%) on farmlands used for livestock grazing, maize and seed potato production and pastures for fodder and agricultural practices is made up of Vlei rats (*Otomys spp.*). The next most common prey species is small birds, with the flufftail (*Sarothura spp.)* being preyed upon the most (Bowland 1990). Other ancillary prey species include small and juvenile wild antelopes, reptiles, genets (*Genetta spp.)*, hares (*Lepus spp.)* and arthropods (Ramesh and Downs 2015b; Hunter 2018). Ramesh and Downs (2015b) found that reptiles and insects ranked low in the diet of serval and suggested that consumption of insects may be opportunistic. Diet preference is based on prey abundance (Geertsema 1985; Bowland 1990; Ramesh and Downs 2015b) and when preferred prey are scarce, serval have been documented predating on species that are possibly more energetically costly and risky to catch including the fawns of reedbuck (*Redunca spp.)* and duiker (*Sylvicapra, spp*.) (Sunquist et al. 2002; Ramesh and Downs 2015b). On average, serval males are 20-30% larger than females (Bowland 1990; Ramesh and Downs 2015b) allowing the former to capture larger prey items (Ramesh and Downs 2015b).

Livestock depredation is notably rare, but occasionally servals have been reported predating on domestic poultry and young lambs (*Ovis aries*, Bowland 1990; Bowland and Perrin 1993; Thiel 2015; Hunter 2018). Despite the irregularity of serval predating on livestock and poultry, they are still persecuted by farmers as a perceived livestock threat (Thiel 2015). Servals may be beneficial to crop farmers by playing a role in population regulation of rodent pests in agricultural landscapes (Ramesh and Downs 2015b).

When hunting, the serval uses its long neck to raise its head high above the vegetation and its large, oval-shaped ears to locate prey by detecting their movement (Geertsema 1985). Once prey is detected, the serval will listen intently to pinpoint the exact location. If the prey is a few metres away, the serval will slowly move forward in a stalking position. It will then use its long legs to jump up to four metres in distance and over a metre in height (Smithers 1978; Geertsema 1985) with the goal of an aerial pounce. Geertsema (1985) observed servals switching technique to a series of zig-zagging pounces while following an escaping rodent if the initial pounce was unsuccessful. Servals will use their front legs to deliver forceful blows to kill prey, both on the ground and in mid-air. Geertsema (1985) also recorded a juvenile male investigating bird nests by standing on its hind legs and using its front paw to poke inside and investigate holes (nests) in a river embankment.

Conservation Status

A lack of data and their broad range means that servals are listed as least concern by the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (Thiel 2015). This status, however, likely requires revision, as there is a scarcity of basic population information and the extent and consequences of habitat loss and/or fragmentation for this species are not yet entirely understood (Thiel 2011; Thiel 2015; Manqele et al. 2018). Status assessments must rely on expert opinion of trends in population abundance or geographic range when in-depth population information is scarce (Mace et al., 2018; Petersen et al., 2019). Expert opinions can be subjective and population dynamics can vary widely across a species' range which can lead to an inaccurate assessment of species' status (Regan et al., 2005; Petersen et al., 2019).

In South Africa, servals are protected under section 56 of the National Environmental Management and Biodiversity Act (NEMBA) No. 10 of 2004 (Manqele et al. 2018). Furthermore, according to the KwaZulu-Natal Nature Conservation management Amendment Act no. 5 of 1999, the serval is a specially protected indigenous mammal (Manqele et al. 2018), which requires permits to in relation to hunting and the use of animal parts. However, there have not been any permits issued for harvesting servals within open access areas. Manqele (2017) issued questionnaires in KwaZulu-Natal and found that the costs of the permits are the most prohibitive factor and that illegal harvest is likely to be in progress to obtain serval skins.

Threats

Ray et al. (2005) identified ten threats to African carnivores (human conflict, habitat decline, interspecific, disease, genetic, road kill, tourism, insect control, hunting and climate) and then scored their likely severity, the timescale over which they are most likely to impact, probability of occurrence and the geographical extent. Ray et al. (2005) concluded that servals should be listed as a species of concern with habitat decline, human conflict, human hunting and roadkill as the greatest threats servals face (Ray et al. 2005). Ramesh et al. (2016) lists the major threats to servals in South Africa as habitat loss, road mortalities, non-targeted predator persecution and incidental snaring and killing for use in traditional attire and medicine.

The most consistently recognised threat to servals is habitat loss and degradation (Ray et al. 2005; Ramesh et al. 2016a; Hunter 2018). Grasslands are degraded through agricultural practices such as annual burning as well as by over-grazing of livestock which decreases prey populations (Bowland 1990; Ramesh et al. 2016a; Hunter 2018). Draining of wetlands has also had significant impacts on serval populations (Bowland 1990; Hunter 2018). Driver et al. (2012) found that wetlands are the most threatened of all ecosystems in South Africa with 65% of wetland ecosystems types being threatened, and 48% listed as critically endangered (Ramesh et al. 2016a). According to the South African National Land-Cover report, there has been a 32.8% decline in natural wetlands over a 24-year period from 1990-2013/2014 largely as a result of anthropogenic activities but also partially due to overall drier conditions (Ramesh et al. 2016a). However, the loss of wetlands may be counterbalanced by the expansion of “pseudo-wetlands” and dam impoundments (Herrmann et al. 2008; Power 2014; Ramesh et al. 2016a) and the servals’ tolerance of anthropogenically-altered landscapes (Loock et al. 2018).

Servals are commonly reported as roadkill in South Africa (Ray et al. 2005; Ramesh et al. 2016a; Williams et al. 2019). Williams et al. (2019) examined roadkill counts along a 410 km stretch of the N3 road in South Africa between 2014 and 2017 and noted that servals were the most common carnivore carcass found. The section of the N3 which contained the most serval mortality, cut through preferred serval habitat. Williams et al. (2019) suggested that the percentage of wetlands near roadways may be the best predictor of serval road mortality. Stott (1980) also proposed that servals may be drawn to road edges because increased rain runoff from hard surfaces promotes good grass cover which in turn attracts small mammals. Servals tend to freeze when faced with oncoming headlights increasing their susceptibility to being struck by a vehicle (L. Hunter pers. obs., Ray et al. 2005). There is little information on the impact that road mortality has on serval populations (Ray et al. 2005).

Servals are targeted by farmers as a potential threat to livestock despite limited evidence that servals regularly kill domestic animals (Smithers 1978; Bowland 1990; Ray et al. 2005). Additionally, direct persecution of servals occurs for the fur trade along with the use of whole skins for traditional and religious attire. Servals are also traded as live animals for pets and animal viewing facilities (Ray et al. 2005; Ramesh et al. 2016a).

The CITES trade data for serval exports recorded 761 live servals and 154 trophies from 2002 to 2017 (CITES Trade Database, UNEP World Conservation Monitoring Centre, Cambridge, UK) with a noticeable increase in the number of live servals exported annually from 2014 onward. Serval can become docile as kittens making them attractive as pets (Pienaar et al. 1996). They can interbreed with feral cats and have been deliberately hybridised with domestic cats creating a newly registered breed with the International Cat Association called the “Savannah cat” (Eckermann-Ross 2014; Ramesh et al. 2016a). However, male Savannah cats become infertile after a few generations (Davis et al. 2015) and pure servals need to be bred back into the gene pool. The demand for captive servals and serval hybrids for the pet industry may include extractions from the wild, but this has yet to be studied and the impact of international trade in live servals on wild populations is currently unknown (Ramesh et al. 2016a).

Throughout Africa, the serval is a common species in the local fur and parts trade for ceremonial and medicinal purposes (Ray et al. 2005; Hunter 2018). Serval furs have also been used in lieu of leopard and cheetah (*Acinonyx jubatus*) skins which are typically more sought after and command a higher price by tourists (Nowell and Jackson 1996). Ceremonial use for serval furs is also popular (Ray et al. 2005). Panthera (2019) reported furs from approximately 800 servals at the 2018 Kuomboka festival in Zambia. Serval body parts are particularly sought after in domestic medicinal trade to cure urinary problems and epilepsy (Kingdon 1971; Manqele 2017). Due to their relatively small size they are harvested in large quantities to ensure profitable sales in these markets (Manqele 2017). At present little is known with regards to the number of servals used for traditional purposes annually and the potential impact this may have on populations (Manqele 2017).

A review of the scientific literature on servals

Serval range is thought to extend to 41 countries (IUCN 2016, see Figure 4), but density estimates (Table 1) are currently limited to Namibia (Edwards et al. 2018), Senegal (Kane et al. 2014), portions of South Africa (Ramesh and Downs 2013; Loock et al. 2018), Tanzania (Geertsema 1985), the Republic of Congo (Bohm and Hofer 2018) and Zambia (Thiel 2011). Published density estimates for sub-Saharan Africa range widely, from 0.63 – 1.28/100 km^2 in Namibia (Edwards et al. 2018) and from 62.55 to 111.55/100 km^2 in South Africa (Loock et al. 2018). The latter estimate is likely to be an artefact of the area being a high security manufacturing plant with ideal habitat for serval combined with limited poaching, the absence of any large predators and artificial water bodies (Loock et al. 2018). Bohm and Hofer (2018) reported a density of 10.37 – 11.81/100 km^2 in the Republic of Congo's Odzala-Kokoua National Park, Kane (2014) reported a density of 2.51 – 2.82/100 km^2 in Senegal and Thiel (2011) reported a density of 9.90/100 km^2 in Zambia's Luambe National Park.

Table 1. Summary of published serval density estimates throughout their range.

Country	Location	Date	Method	Intertrap Distance	No. of Stations	Individuals	Analysis	Density Estimate	Sigma	Target Species
Tanzania[1]	Ngorongoro Crater	1977-1981	Obs	n/a	n/a	Estimated 19-75	n/a	41.67	NA	Servals
Zambia[2]	Luambe National Park	2008	CT	1.84 km	20 (single)	7	CR	9.9	NA	Servals
South Africa[3]	Drakensberg Midlands	2012-2013	CT	1.5 km	44 (single)	13	ML SECR	6.2 ± 2.7 – 8.2 ± 2.6	1.0 km – 1.78 km	Servals
							Bayes SECR	6.0 ± 1.8 – 8.3 ± 1.8	0.11 km	
Senegal[4]	Niokolo Koba National Park	2013	CT	2.5 km	28 (dual)	10	ML SECR	3.49 ± 2.47	1429 m	Lions, leopards and servals
							Bayes SECR	4.74 ± 2.94		
Republic of Congo[5]	Odzala-Kokoua National Park	2013-2014	CT	2.7 km	38 (single)	51	ML SECR	9.8 ± 2.1	2226 m	Spotted hyenas
							Bayes SECR	7.7 ± 1.2	1239 m	
Namibia[6]	Khaudum National Park	2014	CT	2.65 km	29 (dual)	10	Bayes SECR	1.28 ± 0.23	5890 m	Leopards
	Mudumu North Complex	2014	CT	3.20 km	29 (dual)	9	Bayes SECR	0.63 ± 0.51	4710 m	Leopards
South Africa[7]	Secunda Synfuels Operations Plant	2014-2015	CT	1.2 km	34 (single)	61	ML SECR	62.33 ± 16.03 - 111.55 ± 22.76	268 m	Servals

[1]Geertsema 1985, [2]Thiel 2011 , [3]Ramesh and Downs 2013 , [4]Kane et al. 2014 , [5]Bohm and Hofer 2018 , [6]Edwards et al. 2018 , [7]Loock et al. 2018, Method, obs, visual observation or CT, camera trap; Number of stations, single or dual camera trap stations; Analysis, CR, capture-recapture, ML SECR, Maximum likelihood spatially explit caputre recapture, Bayes SECR, Bayesian spatially explicit caputre recapture; Density estimate servals/100km^2

The methods used to provide density estimates for servals vary widely. Geertsema (1985), Thiel (2011), Ramesh and Downs (2013), Ramesh et al. (2016b) and Loocke (2018) designed studies specifically for servals. Kane et al. (2014), Edwards et al. (2018), Bohm and Hofer (2018) all utilised data collected from surveys designed for larger carnivores to ascertain density estimates for servals as by-catch. From November 1977 to October 1981, Geertsema (1985) tracked and observed habituated servals from a four-wheel drive vehicle in the Ngorongoro Crater, a protected UNESCO World Heritage Site in Crater Highlands of Tanzania. Servals were identified by their unique stripe and spot pattern and followed for observation. The aim was to record continuous 12- or 24-hour follows, but due to the rough terrain, observation periods varied from only a few minutes to several hours. Geertsema (1985) suggested that the abundance and availability of prey were the primary determinants of serval home range. Serval home ranges in the Ngorongoro Crater overlapped with males having larger ranges that encompassed multiple smaller female home ranges but having little overlap with other males' ranges. Despite spatial overlap, servals were rarely found to use the same space in time and thus avoided direct encounters with conspecifics. Although Geertsema's methods are no longer used making direct comparisons with contemporary studies difficult, she did provide density estimates: 1 serval/2.40 km for an estimated 19-75 individuals within 80 km^2 of 'optimal' habitat giving a rough density estimate of 41.67 servals/100 km^2.

Thiel (2011) used camera traps to estimate abundance of servals in Luambe National Park in the Luangwa valley, Zambia. Her survey was comprised of 20 automatic digital camera traps positioned at single camera stations with an intertrap distance of 1.84 km ± 0.14 km covering 40.40 km^2. Camera stations were mainly placed along game trails (70%) in habitats deemed to be more optimal for servals (Thiel 2011). The cameras were active for 24 hours a day for 74 consecutive days. During Thiel's survey, four cameras (20%) captured seven serval images consisting of four individually recognisable adult servals, with three recaptures. Servals were identified by the unique patterns on their tail, shoulder, hip and leg regions. Total abundance was calculated using the programme CAPTURE (Otis et al. 1978, updated by Rexstad and Burnham 1992) based on the number of individuals identified. The study reported a density of 9.90

servals/100 km^2, although no recaptures occurred at different locations and few individuals were captured overall. The programme CAPTURE uses standard mark-recapture techniques. In non-spatial capture-recapture methods, density is estimated by deriving a survey area sampled by the camera traps that is bounded by a buffer based on either the ½ or full mean maximum distance moved (MMDM) by individuals captured by the camera trap (Karanth and Nichols 1998; Noss et al. 2012). Due to the *ad hoc* nature of estimating the buffer, non-spatial capture-recapture models can be inherently biased.

Ramesh and Downs (2013) conducted field surveys between July 2012 and January 2013 in a survey to determine if servals were less active diurnally due to intensive farming in the area in the Drakensberg Midlands, South Africa. A systematic two-kilometre squared camera trap grid system was designed based on serval spoor surveys, proximity to wetlands and knowledge of serval presence provided by local landowners. The grid size was based on data collected from a radio collared serval study in KwaZulu-Natal, which found serval home range to be 15-30 km^2 based on data collected from six individuals (Bowland 1990). A camera spacing of two kilometres was thus thought to be sufficient to have at least two trap stations per serval home range (Bowland 1990; Dillon and Kelly 2008; Ramesh and Downs 2013). The survey was comprised of 44 single camera trap sites recording for a period of 30 days across three sites of varying farming intensity. Cameras were placed along paths and game trails with an average intertrap distance of 1.50 km. Serval spot patterns are asymmetrical between the left and right flanks of an individual, and thus left and right flanks were identified and analysed separately. Ramesh and Downs (2013) identified 12 individuals from the left flank and 13 individuals from right flank. No major variations in the abundance of serval were apparent between sites leading to the conclusion that servals readily adapt to anthropogenic disturbance which may promote prey populations. The study estimated serval densities at 6.2-7.7 servals/100 km^2 averaged across the three different sites. Ramesh and Downs (2013) recommended that future studies reduce intertrap spacing and use a maximum grid size of 1-1.5 km^2 along with paired camera stations.

Kane et al. (2014) conducted a camera trap survey looking at population size and density of lions, leopard and servals in Niokolo Koba National Park in Senegal. A pilot study was conducted placing five camera stations along human paths and 20 stations along game trails. The majority of the carnivore captures occurred on roads and it was decided to use only management and tourist roads for the study. The study placed 28 dual camera trap stations (both digital and film camera traps) along roads with an intertrap distance of 2.5 km. The survey ran for a total of 78 days. Nine individual servals were identified from right flanks and 10 individuals were identified from left flank images with more recaptures from the right flank database. Kane et al. (2014) used the ML SECR programme, 'DENSITY' and the Bayesian SECR package ''SPACECAP'' to estimate serval densities of 3.49 – 4.73 servals/100 km^2 using 'DENSITY' and 2.70 – 2.82 servals/100 km^2 using 'SPACECAP'. The study also reported that servals selected habitats with denser canopy cover where leopards were absent.

Bohm and Hofer (2018) camera trapped in the forest-savannah mosaic of Odzala-Kokoua National Park in the Republic of Congo. The survey was designed for a spotted hyena (*Crocuta crocuta*) population survey and the camera trap stations were placed into 38 3.5 km grid cells with most stations having one camera per station and an average intertrap distance of 2.7 km. Cameras were programmed to take five photographs per trigger event without a delay between triggers which provided a large number of photographs of each individual and allowed for sex to be identified. Bohm and Hofer also compared temporal activity patterns of servals and the park's dominant predator, spotted hyenas. They identified 51 serval individuals, and 69% of the individuals recorded were of the servaline morph with small, "freckled" spots. Bohm and Hofer (2018) were able to identify 17 male and 25 female servals with six spatial recaptures, which is when an individual was detected at a different station location from the original detection station. The low spatial recapture rate, especially for females may be due to large intertrap distance. The R packages 'secr' 3.1.1 (Efford 2011) and 'SPACECAP' 1.1.0 (Gopalaswamy et al. 2012a) were used for analyses. 'SPACECAP' (Gopalaswamy et al. 2012a) produced a density estimate of 9.8 servals/100 km^2 and 'secr' (Efford 2011) produced a density estimate of 7.7 servals/100 km^2. The study found that male and female servals showed different activity patterns with 59% of male servals being active mainly during the night compared to 78% of females which were mainly active during daylight hours. The study also showed that spotted hyenas were highly nocturnal and the coefficient of overlap with male servals was 0.72 (CI = 0.64–0.78), and 0.38 with female servals (CI = 0.31–0.45). Female servals raise their young alone and larger predators have been known to prey on young servals. The significantly lower overlap between female servals' activity pattern and spotted hyenas' led to the suggestion that female servals may be actively avoiding spotted hyenas (Bohm and Hofer 2018).

A camera trap survey was deployed as part of a leopard project in Khaudum National Park and in the Mudumu North Complex in Namibia (Edwards et al. 2018) with serval densities analysed as by-catch of the leopard survey. The survey consisted of multiple sites with 37 dual camera trap stations at Khaudum National Park. The Mudumu North Complex was split into three blocks: 34 stations were set up at two blocks and 29 stations for the third block. The mean intertrap distance varied from 2.65 km to 3.20 km between the sites. Camera trap stations were positioned along roads and game paths and the surveys ran for 70 to 81 days. In Khaudum National Park, 10 individual servals were identified with three spatial recaptures. Edwards et al. (2018) used 'SPACECAP' with a 10 km buffer to producing serval density estimates of 1.28 servals/100 km^2. At the Mudumu North Complex, nine individual servals were identified with a density estimate of 0.63 servals/100 km^2. Edwards et al. (2018) suggested that interference competition from sympatric carnivores may explain the low density estimates. All of the sites have resident populations of leopards, lions and spotted hyenas which have all been recorded as occasionally killing young and adult servals (Hayward et al. 2006; Thiel 2011).

Loock et al. (2018) placed 34 camera traps at the 50 km^2 secondary perimeter area surrounding the primary petrochemical plant of Secunda Synfuels Operations plant in Mpumalanga province, South Africa. Three separate surveys with camera traps placed on roads and game paths (intertrap distance of 1.2 km) ran sequentially for 40 days each. Loock et al. (2018) also conducted live trapping of servals to record the capture rate and population structure using baited steel trap cages. 61 servals were identified from the camera surveys and data were analysed using the 'secr' package (Efford 2011) in Program R. Density estimates of 66.33-111.55 servals/100 km^2 were obtained with vegetation type having a significant effect on serval encounter rates. Grassland habitat had the lowest encounter rate with wetlands having the highest (Loock et al. 2018). 65 individual servals were captured in the live trapping survey with four recaptures comprising of 26 adult males, 19 adult females and 18 subadult and juveniles.

Between May 2013 and August 2014, Ramesh et al. (2016b) captured, immobilised and GPS collared a representative sample of servals from populations in the Midlands, KwaZulu-Natal to determine home range size, movements and habitat selection. They captured sixteen servals (11 males and five females) ranging in age from two to five years old and fitted the individuals with radio collars. Similar to Geertsema (1985), they found considerable home range overlap between the sexes but little overlap with same sexed individuals (Ramesh et al. 2016b). Using Manley's selection index, wetland habitats were ranked the highest for habitat use of both sexes followed by forest with bushland, grassland, plantations and croplands which were avoided. Interestingly, Ramesh et al. (2016b) found that male servals frequent forest habitat two times more often than females. Males home range estimates with 95% fixed kernel density were 38.07 km^2 while females home range estimates were smaller at 6.22 km^2 in the Midlands. Bowland (1990) estimated minimum convex polygon home ranges of 2.2-31.5 km^2 for males and 15.8-19.8 km^2 for females using relatively low numbers of very high frequency (VHF) positions in a previous study in the Midlands of KwaZulu-Natal.

Motivation for this study

Servals are thought to be declining throughout their historical range (Ramesh et al. 2016a) as this species is threatened by habitat loss and degradation (Ramesh and Downs 2013), incidental poisoning (Ramesh et al. 2016a), illegal fur trade (Ramesh et al. 2016a; Manqele et al. 2018), as well as retaliation for poultry predation (Thiel 2015; Manqele et al. 2018). Furthermore, populations may also be threatened by a burgeoning pet trade and hybridization with domestic cat breeds (Ramesh et al. 2016a). Given these impacts, there is an urgent need for long-term monitoring of populations within both formally protected as well as unprotected areas to establish population trends in areas with limited habitat loss and transformation. Density estimates are undoubtedly the most useful population parameter for understanding how populations within particular areas fluctuate through time (Thiel 2011; Edwards et al. 2018). Long term surveys of cryptic carnivores are, however, rare with research being heavily biased towards large, charismatic and threatened species.

The main motivation for this study was to improve our understanding of the accuracy of using survey girds designed for large carnivores to gain insight on serval population demographics within a protected area. I selected Ithala Game Reserve (hereafter referred to as Ithala) in KwaZulu-Natal as my study site because, historically, it has been the reserve with the most serval detections on the annual Panthera leopard surveys (Mann pers. comm.). Panthera has performed leopard surveys in Ithala using paired camera traps at 29-36 stations with a mean inter-trap distance of approximately 2.3 km for seven consecutive years (2013-2019). This presents a unique opportunity to investigate how serval density has varied across time within this protected area and potentially in all the other reserves currently being monitored by Panthera in South Africa (n=30). However, it is possible that estimating serval density using data collected from a survey designed for a large predator (leopards) may result in too few captures and recaptures and hence poor density estimates. I thus ran a serval-specific survey with a smaller inter-camera trap distance simultaneously with the standard leopard in one of the years (2019). I then compared the density estimates for both the leopard and serval specific arrays for both leopards and serval to understand the effects of inter-camera distance and placement on density estimates for a large and medium sized carnivore in a protected area. Based on these findings I was able to justify the use of the long-term leopard array to provide annual density estimates for servals from 2013-2018. I also fit covariates to these data to explore possible drivers of serval density in Ithala in addition to assessing the naïve occupancy of other wildlife species detected on both the serval and leopard arrays.

2. Description of study site

Study Area

Preliminary density estimates on servals from Panthera camera traps showed that Ithala Game Reserve had the highest and most reliable number of serval captures across multiple years making it the ideal reserve on which to conduct my serval-specific survey. Ithala is 29 653 hectares and is situated between the town of Louwsburg and the Phongolo River in northern KwaZulu-Natal, South Africa with geographical co-ordinates 27°30' S, 31°25' (Ezemvelo KZN Wildlife 2009).

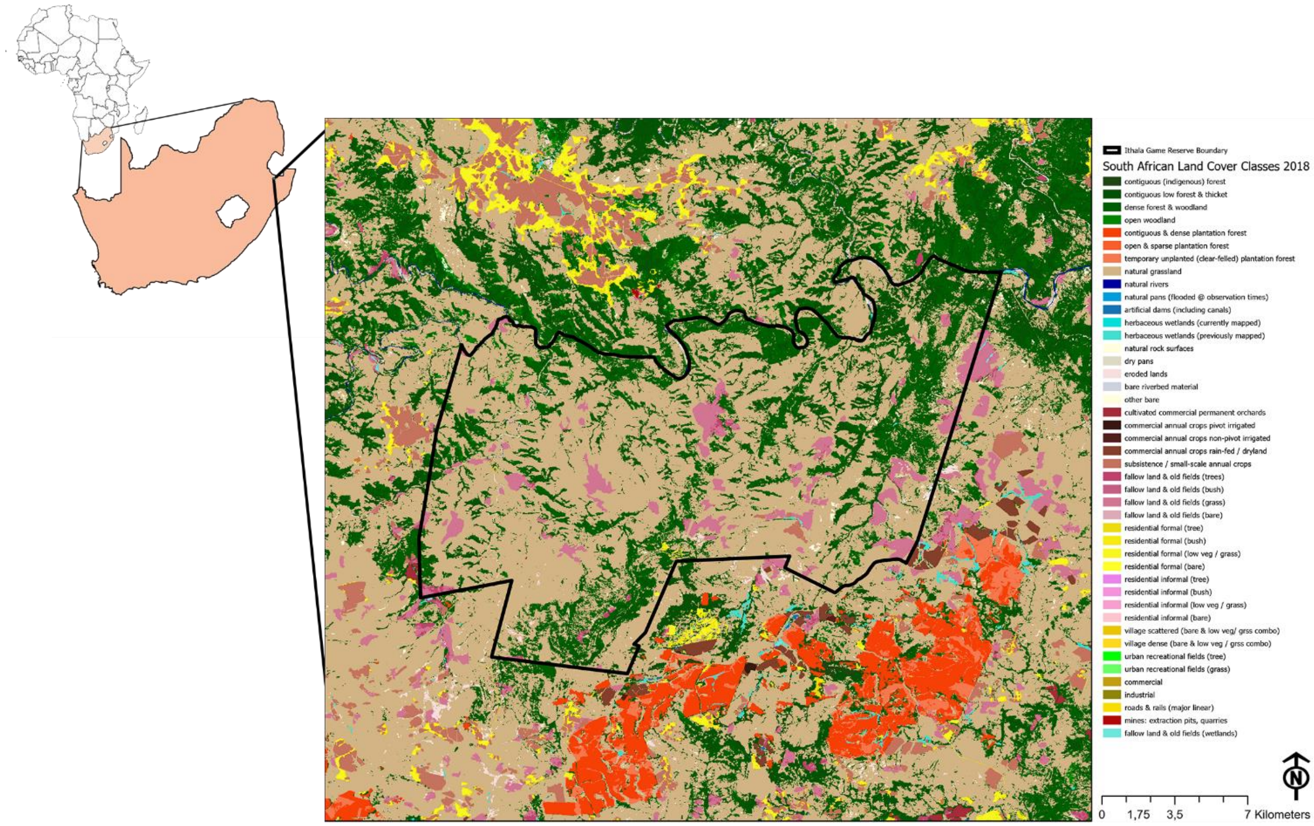

Figure 5: Ithala Game Reserve is found in KwaZulu-Natal province of South Africa showing the South African National Land-Cover (SANLC) 2018 classes.

The northern boundaries are bordered by Traditional Authority areas, commercial landowners neighbour the eastern and western boundaries, and the town of Louwsburg along with commercial landowners border the southern boundary (Ezemvelo KZN Wildlife 2009). Ithala has a network of tar and gravel roads, as well as small camps, a lodge, picnic sites, staff accommodation and park management infrastructure. The eastern portion of the reserve is the least developed with only private 4x4 tracks and private accommodation, while the western portion has more tourism and management infrastructure. The reserve is fenced on three of its boundaries, the northern boundary of Ithala is bordered by the Phongola River and is not fenced.

History

Ithala Game Reserve is named from the Thalu River and the word "ithala" which means "hidden shelf where valuables are stored" in Zulu (Ezemvelo KZN Wildlife 2009). Ithala was established as a game reserve in 1973 in accordance with Section 15 of the Nature Conservation Ordinance, 1974 (Act No. 15 of 1974) and the KwaZulu-Natal Nature Conservation Management Act, 1997 (Act No. 9 of 1997) (Ezemvelo KZN Wildlife 2009).

Prior to being established as a game reserve, the land was part of the "Nieuwe Republiek" a 1.1 million hectare piece of land that was bestowed on the boers in 1884 by King Dinizulu in recognition of their fighting service (Ezemvelo KZN Wildlife 2009). The combined effects of farming, hunting, disease outbreaks and the persecution of wildlife that provided hosts for nagana or sleeping sickness (*Trypanosomiasis spp*) had a drastic impact on the indigenous wildlife with 25 mammal species becoming locally extirpated (Ezemvelo KZN Wildlife 2009; Valls Fox et al. 2015). Most of the farmlands were used as tenant, or labour farms for maize (*Zea mays*) and cotton (*Gossypium hirsutum*) crops that were grown in the flatter sections of the reserve (Wiseman 2001). Overgrazing by livestock caused extensive damage to the vegetation and resulted in extensive and severe soil erosion. The initial proclaimed reserve, consisting of 8 000 hectares was fenced and the damaged veld was left to recover (Johnson 1990).

Fauna

Conservationists and reserve managers used records from the nearby Pongola Reserve to determine which species to reintroduce into Ithala (Ezemvelo KZN Wildlife 2009). A total of 23 mammal species were reintroduced including black rhinoceros (*Diceros bicornis L.*), white rhinoceros (*Ceratotherium simum*), impala (*Aepyceros melampus*) and greater kudu (*Tragelaphus strepsiceros*) (Wiseman 2001). Between 1990 and 1994, 50 elephants (*Loxodonta Africana*) were introduced and have since successfully bred (Wiseman 2001). Ithala's mammal checklist currently includes 38 mammal species and 323 bird species (Ezemvelo KZN Wildlife 2009). Black-backed jackals, leopards, brown (*Hyaena brunnea*) and spotted hyenas, servals and even two wild dogs have recolonised the reserve and were detected during our camera trap surveys. However, according to Ezemvelo KZN Wildlife, inadequate fencing has prevented the reintroduction of lion, by management into the reserve.

Topography and Geology

Elevation ranges from 320 m above sea level at the lowest point along the Phongola River in the north to the highest point at 1446 m above sea level at Ngotshe Mountain (van Rooyen and van Rooyen 2010). Ithala's varied topography comprises mountains, plateaus, low hills and ridges, plains and valleys. van Rooyen and van Rooyen (2010) quantified the different topographies in the reserve as a proportion of the total area with moderate and steep sloped land together with foot slopes comprising 80% of all land (Table 2).

Table 2. Topography types and total area coverage in Ithala Game Reserve, South Africa.

Topography	Total Area	Percentage
Drainage lines/wetlands:	2019 ha	(7%)
Plains and foot slopes	10659 ha	(36%)
Undulating moderate to steep slopes	13812 ha	(46%)
Ridges, rocky outcrops	1708 ha	(6%)
Scarp, cliffs, kloofs	1068 ha	(3.7%)
Mountain plateau	387 ha	(1.3%)

The majority of Ithala's undulating topography is underlain by Archaean rocks and the most common of sedimentary rocks alternate with shales and quartzites (van Rooyen and van Rooyen 2010). These underlying rocks form the soils found in Ithala with the more resistant quartzite rocks forming ridges which occur as parallel, generally north–south trending bands, except in the central region of the reserve where they trend east–west (van Rooyen and van Rooyen 2010). In the higher elevation sections found in the southern part of the reserve, sedimentary rocks of the Karoo Supergroup occur (van Rooyen and van Rooyen 2010). The cliffs of the Ngotshe Mountain are formed from thick dolerite sills which produce fertile soils (van Rooyen and van Rooyen 2010). Soils at higher elevations tend to be leached, while the soils of valley bottoms are more fertile with higher clay contents.

Precipitation and Temperature

Rainfall is seasonal peaking in the summer months (October to March) when more than 80% of the total annual rainfall occurs. June to August are the driest months, with less than 20 mm of rain per month recorded on average (van Rooyen and van Rooyen 2010). Annual rainfall recorded over 37 years ranged from 394 mm in dry years to 1164 mm per annum during exceptionally wet years, with a mean annual rainfall of 763 mm (Valls Fox 2015). The altitudinal variation and topography cause precipitation to vary with localised rain shadows (Ezemvelo KZN Wildlife 2009). There are three general rainfall areas recognised in the reserve: the southern mountain plateau where the annual rainfall is in excess of 940 mm, the central plateau of lower elevation where the rainfall is between 800 and 870 mm, and the northern dry valley lowlands where rainfall is generally less than 750 mm per annum (van Rooyen and van Rooyen 2010).

The area experiences warm to hot summers with daily mean temperatures of 18 to 30°C with maximum temperatures up to 40°C. Winters are mild with daily temperatures averaging 15-25°C (Porter 1983; Greaver et al. 2014). Although, temperatures can reach near freezing on cold winter nights, especially at the high altitudes, frost does not occur (Porter 1983).

Vegetation

Ithala falls in both the Grassland and Savannah Biomes (Rutherford and Westfall, 1994). The vegetation can be classified into three broad structural classes: bushveld/thicket, which makes up 52.4% (15,478 ha), grassland/wooded grassland at 36.8% (10,865 ha), and forest at 2.3% (671 ha). Riparian areas cover approximately 8.5% (2 500 ha) and built-up areas cover 0.2% (45 ha) of the reserve (van Rooyen and van Rooyen 2010). The grasslands of Ithala were extensively farmed prior to the reserve being proclaimed which has altered the chemical composition of the soils. Grass species that become unpalatable when mature have mostly recolonised the disturbed lands (van Rooyen and van Rooyen 2010).

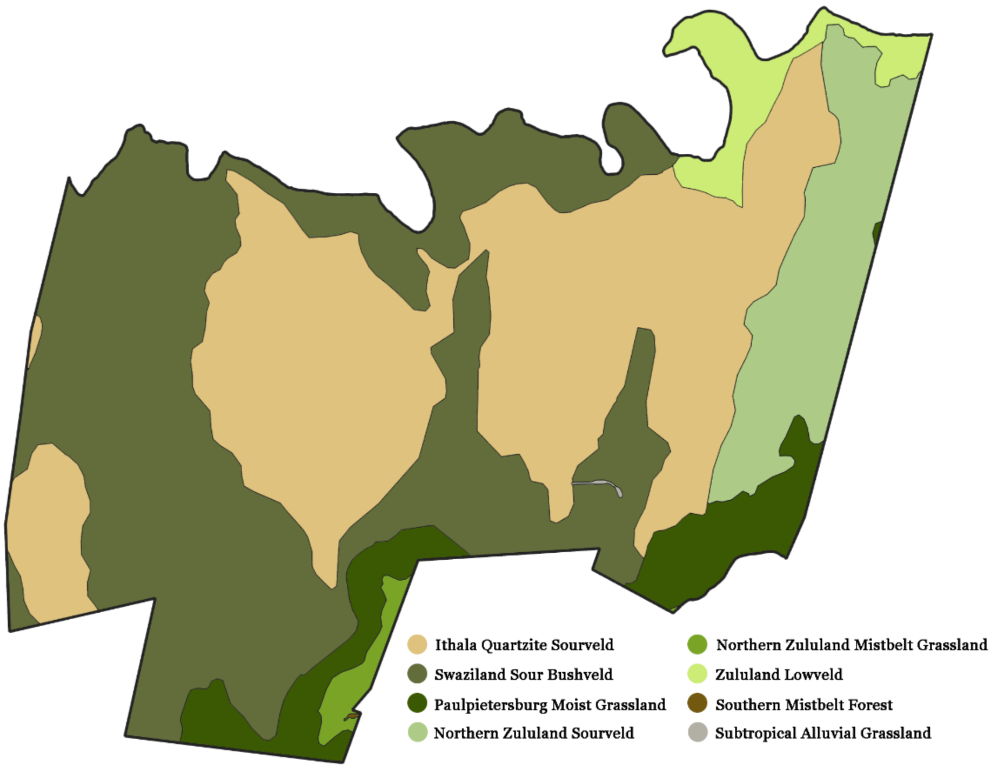

Figure 6. South African National Biodiversity Institute (2012) vegetation map of Ithala Game Reserve

According to the South African National Biodiversity Institute (2012) the following vegetation types occur in Ithala: Northern Zululand Mistbelt Grassveld, Ithala Quartzite Grassveld, Swaziland Sour Bushveld, Northern Zululand Sourveld, Paulpietersburg Moist Grassland, Northern Zululand Misbelt Grassland, Southern Mistbel Forest, Zululand Lowveld and Subtropical Alluvial Grassland (see Figure 6). The Ithala Quartzite Grassveld covers the majority of the reserve and is found over large quartzite patches which are characterised by undulating hills and low mountain ranges with a poorly developed grass layer (van Rooyen and van Rooyen 2010). The grass layer is dominated by *Hyperthelia dissoluta, Heteropogon contortus, Loudetia simplex, Themeda triandra, Trachypogon spicatus, Diheteropogon amplectens* and *Pogonarthria squarrosa* (van Rooyen and van Rooyen 2010). 37% of our serval array camera trap stations were placed with in the Ithala Quartzite Grassveld vegetation type. The Swaziland Sour Bushveld covers the central part of the reserve with a well-developed grass layer. The majority of our camera trap stations (41%) were placed within Swaziland Sour Bushveld. The dominant grass species are *Themeda triandra, Panicum maximum, Sporobolus fimbriatus* and *Sporobolus nitens*. The forb layer is characterised by *Becium obovatum, Gerbera viridifolia, Hemizygia pretoriae* and *Hypoxis rigidula* (van Rooyen and van Rooyen 2010).

3. Methods

Camera trapping

Due to the elusive and typically crepuscular and/or nocturnal nature of servals, direct count observation censuses are not possible, and monitoring can be a challenging endeavour. Other population monitoring methods such as GPS or VHF telemetry tracking collars and capture-recapture methods are not only invasive to the target animals but are a more costly in both monetary expense and researcher time. Other methodologies include non-direct observation methods such as sign surveys including spoor counts (Smallwood and Fitzhugh 1995; Staender 1998), scat counting (Cavallini 1994; Webbon et al. 2004) and den enumeration (Wilson et al. 1997; Barea-Azcon et al. 2007). Another method which are routinely used in North and South America for relative abundance estimates include track plate surveys using scent stations which consists of a scent lure and a tracking medium such as sand or soft soil or a track plate (Sargeant et al. 2003). Both sign surveys and track stations are limited to identifying species, but not individuals (Sargeant et al. 2003; Barea-Azcon et al. 2007) without further genetic sampling which greatly increase the cost of the project. Although sign survey and track stations are generally low-cost and non-invasive, they have been criticised about their accuracy for population estimates (Barea-Azcon et al. 2007).

In response to similar challenges for other carnivore species, motion-triggered remote camera traps have been used with great success. When this tool is used on species with individually identifiable pelage markings such as spots or stripes, individual recognition is possible allowing for density estimates using the mark-recapture statistical framework. Karanth (1995) used camera trapping to record captures of individually identifiable tigers (*Panthera tigris*) allowing for abundance estimates. Similar studies have been conducted on numerous other uniquely marked cat species (Royle et al. 2013) such as jaguars (*Panthera onca*) (Silver et al. 2004), Geoffroy's cats (*Oncifelis geoffroyi*) (Cuellar et al. 2006), leopards (Balme et al. 2009), cheetahs (*Acinonyx jubatus*) (Marnewick et al. 2008), bobcats (*Lynx rufus*) (Clare et al. 2015) European wildcats (*Felis silvestris silvestris*) (Anile et al. 2012) and ocelots (*Leopardus pardalis)* (Dillon and Kelly 2008; Satter et al. 2019). Camera trapping methods, in conjunction with spatial capture-recapture models, are one of the most effective methods for obtaining demographic data on rare and elusive species (Royle et al. 2013; Rocha et al. 2016; Satter et al. 2019). An understanding of the interactions and mechanisms governing serval population demographic parameters, especially abundance and density, will prove essential to their conservation, long-term management and the development of protective policy (Dalerum et al. 2008; Royle et al. 2013; Winterbach et al. 2013; Ramesh et al. 2016a; Satter et al. 2019).

In partnership with the various provincial conservation authorities, Panthera initiated the South African Leopard Monitoring Project in 2013. The project uses camera trap surveys undertaken at regular intervals at key surveillance sites to track changes in leopard population density over time. While the focus of Panthera's surveys are leopards, the monitoring framework provides valuable data that might be used to monitor the populations of other species such as servals, cheetahs, and hyenas.

Serval and other mesocarnivores are often only recorded as by-catch in camera trap surveys designed for larger carnivores (Bohm and Hofer 2018). To understand the limitations of such surveys for estimating the abundance and density of other small carnivores, I created a survey specifically designed for servals and ran this survey in conjunction with a Panthera leopard survey in 2019. Density estimates from the two surveys were compared to assess how camera spacing and placement influences density estimates and the implications this may have for population assessments and long-term monitoring of multiple species from an array designed for a single species. I then used data collected by Panthera from 2013-2019 in Ithala Game Reserve to estimate serval densities and population trends over time.

Survey Design

The Panthera leopard survey comprised of 29 camera trap stations. An additional 20 stations were added for the serval array and were active simultaneously with the original leopard array.

Each camera trap station consisted of two cameras set up on opposite sides of a path to allow for simultaneous photographs of both sides of servals as they walk past (Karanth and Nichols 1998; Silver et al. 2004). While using two cameras per station may reduce the number of active stations especially when camera trap numbers are limited, this approach has been shown to increase survey efficiency as it increases photographic capture rate (i.e. detection failure is reduced). A dual camera design also allows for more individuals of the target species to be identified (Negrões et al. 2012; Mann 2014) which increases the chances of recaptures and with that improved accuracy of density estimates. Key recommendations for spatially explicit capture-recapture (SECR) studies are that the camera trapping polygon is larger than the male home range size of the target species and that camera placement maximises spatial captures and recaptures. In the nearby KwaZulu-Natal Drakensberg midlands, the mean home range of collared servals ranged from five to 60 km^2 (Ramesh et al. 2016b).

The current Panthera leopard survey selects its camera location based on the observed minimum home range size of a leopard in KwaZulu-Natal at 30 km^2 (Fattebert 2014) with an intertrap distance of 2-3 km. For the serval survey, I increased the number of camera traps deployed from the original leopard survey to reduce the intertrap distance to 1.3 km and ensure that a camera trap station is placed within the smallest home range size estimates (1-2 km^2) (Loock et al. 2018) available for serval, thus maximising the probability of detecting all age/sex classes.

Small, as well as big felids show a tendency to walk along clear paths and roads (Dillon and Kelly 2008; Sollmann et al. 2011; Mann et al. 2014; Bohm and Hofer 2018). The leopard survey utilises game trails and roads to maximise the probability of photographing leopards and to facilitate access for camera maintenance, this method was also used with the serval-design (Loock et al. 2018). Additional stations were also placed in habitats preferred by servals such as grasslands and wetlands. Camera traps were mounted on trees or steel poles approximately 40 cm above the ground and located two to four meters from the focal movement pathway. Vegetation that might obstruct the camera's field of view was removed to reduce false triggers. The cameras record a single photograph, with a minimum of a 30-second delay. At night and during low light, they operate with a white light flash, dual cameras were placed offset from each other to stop cameras flashes from trigging each other. Cameras were checked every five to seven days to download photographs, replace damaged or lost cameras, and install new batteries when required.

Paired PantheraCam V4, V5 and V6 cameras were deployed at camera trap stations (30 stations for the leopard array and 49 stations for the serval array, see Figure 7) for 52 days. The majority of the cameras traps, 61%, were placed on tourist roads (6% on main tar roads, 47% on non-tar main tourist roads and 29% on tourist 4x4 roads), 35% of the stations were placed on management and private roads and 4% were placed on game paths. Using Pollock's robust design method, which relies on hierarchical sampling periods (Pollock 1982; Kendall and Nichols 2002), density estimates can be calculated over time. Capture-recapture analysis assumes that the study population is geographically and demographically closed (i.e., no births, deaths, emigration, or immigration) during the primary sampling period, but open between sampling periods. Nested within each primary sampling period are secondary sampling occasions, represented by trap-days or otherwise defined durations.

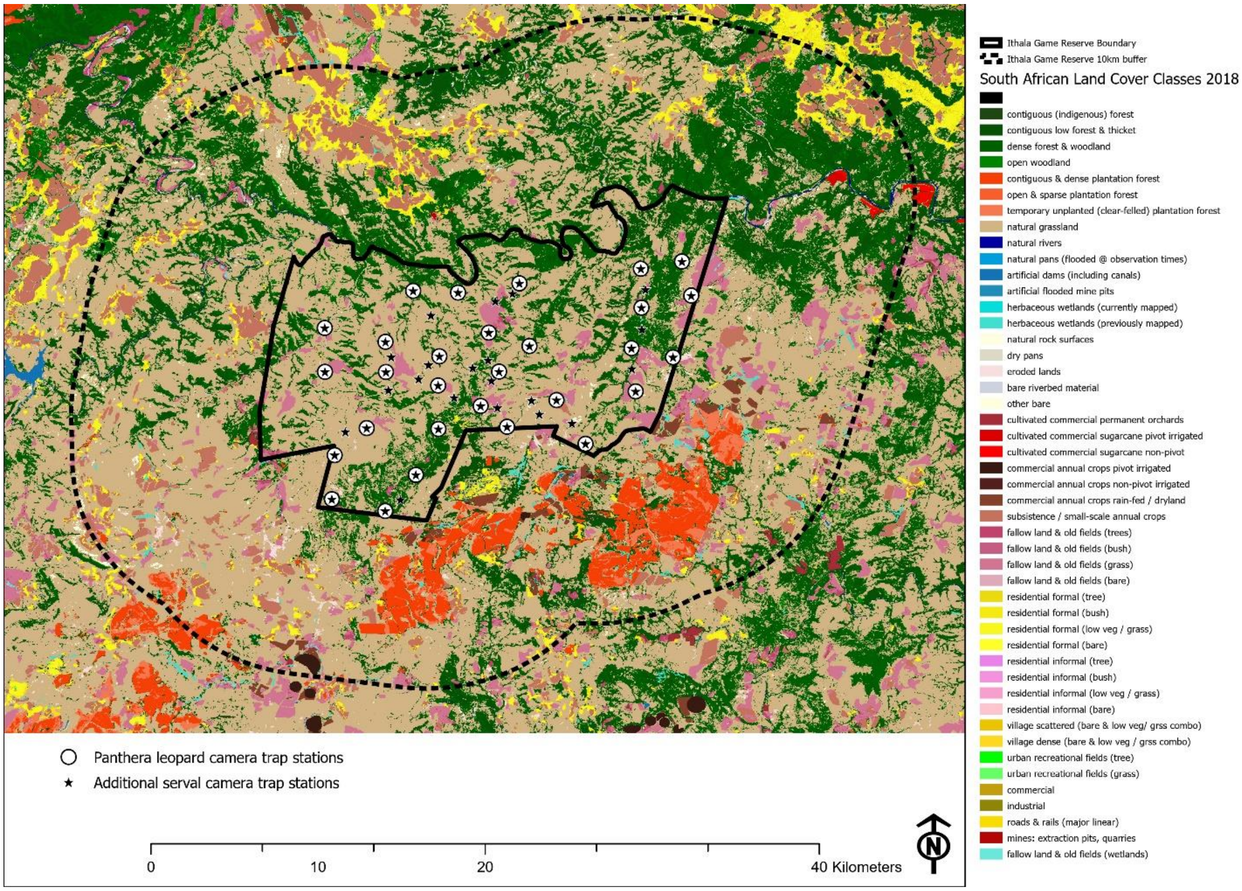

Figure 7: The two survey grids with the white dots representing the original Panthera leopard survey grid and the stars as the more robust serval grid at Ithala Game Reserve including the 10 km buffer the South African National Land-Cover (SANLC) 2018 classes.

Data processing and analysis

Individual servals were distinguished based on their unique pelage patterns using Hotspotter (Crall et al. 2013) pattern recognition software. Hotspotter results were manually verified through visual assessment of the same and different individual identities. Even though all camera trap stations contained two cameras there were still many occasions (n=15, 19%) where only one photograph or only one side of a serval was captured on camera. Instances where a photograph was taken from opposing cameras and individuals were able to be identified with images of both sides were collated. Individuals which were identified from "left-side only" and "right-side only" were similarly collated. The group with the highest number of individuals was then combined with the group which had both-sides for subsequent density analyses. The group with the least number of individuals from a single side were excluded from further analyses to avoid inflating the population estimate. Only independent adult individuals were included in analyses. Blurry photographs and unidentifiable individuals were also excluded from analyses. Recaptures were defined as the total number of detections minus the number of different animals detected (Weingarth et al. 2015).

Trap success was calculated for servals and all large carnivores (leopard, brown hyena, spotted hyena and wild dog) as the number of capture events of each species divided by the total trap nights multiplied by 100 (Dillon and Kelly 2008; Kane et al. 2014). A trap-night was defined as a 24-hour period where at least one of the two cameras was active at each station. Naïve occupancy, the proportion of sites that recorded at least one photograph of a target species, was calculated for each species detected by dividing the number of stations the species was detected at by the total number of stations. Identified individuals (serval and leopard only) were considered to be ‘‘marked” and an individual was considered “recaptured” if it was photographed during more than one capture event. A capture event was defined as photographs captured within a one-hour period of time. A spatial recapture was noted when an individual was recaptured at a different location from the original camera trap location. Capture occasions were represented as each trap day, while capture histories were created by denoting which individual was captured at a specific station, on a given occasion. A trap deployment file was created containing the name of each camera trap station along with its UTM coordinates. A camera activity sheet was created which contained each station name with a “1” for each day of the survey that at least one camera was active and a “0” if both cameras were inactive (the batteries died, camera malfunctioned, camera was knocked over, etc.).The camera traps automatically record the date and time within the metadata of each photo. Using this information, I mapped out the activity pattern overlap of great cane rats (*Thryonomys swinderianus*), the only potential serval prey species recorded during the survey. Whilst there is no empirical evidence to suggest they form the majority part of the diet selection of serval in Ithala, this capture data was used to map out an activity pattern overlap between servals and cane rats.

Density estimates were calculated using maximum-likelihood (ML) (Borchers and Efford 2008) spatially explicit capture-recapture (SECR) models using the 'secr' 3.2.1 package (Efford 2011) and Bayesian-based SECR, using the package 'SPACECAP' 1.1.0 (Gopalaswamy et al. 2012a) in Program R Statistical Environment (R Core Team 2017). The two approaches are common ways of estimating density using spatially explicit capture-recapture. In theory, the results assimilated by both methods should be analogous to each other. By using both ML and Bayesian frameworks, the outputs can be compared to ensure consistency with prior serval studies (Ramesh and Downs 2013; Kane et al. 2014; Bohm and Hofer 2018).

Classical non-spatial, capture-recapture methods may produce biased results when individuals have home ranges that extend past the sample grid which is then not incorporated into the analysis causing inflated density estimates (Karanth 1995; Mann 2014). To amend this, researchers often apply an *ad hoc* buffer around the cameras to derive the total area encompassing the population of interest and divide the estimated abundance by this estimated effective survey area (Bohm and Hofer 2018). This buffer is based on mean maximum distance that the target species may move between camera stations and is calculated as either the half or the full mean maximum distance moved (MMDM) of the species. The MMDM measures are used as a proxy for the home range with the intent to estimate the effective trapping area by buffering the trap array (Noss et al. 2012). However, the maximum distance moved can vary by season, individual and by specific study areas (Noss et al. 2012) and thus, may be greatly influenced by camera spacing (Efford 2004; Maffei and Noss 2008; Foster and Harmsen 2012). Without telemetry data of collared individuals from the specific study area determining the "best" buffer through this method does not have a theoretical mechanism that links abundance with the survey area to estimate density (Williams et al. 2002*;* Noss et al. 2012).This approach can therefore lead to an overestimation of density (O'Brien 2011; Meek et al. 2014; Satter et al. 2019) due to the *ad hoc* nature of estimating the survey area (Noss et al. 2012).

Spatially explicit capture-recapture models are a more robust statistical framework and estimate density directly by using information on capture histories combined with the location of the individual capture. As such they do not require the use of subjective effective trapping areas (Noss et al. 2012; Tobler and Powell 2013; Loock et al. 2018). Spatial models assume that each individual, *i*, in the population has a specific activity centre, $\mathbf{s}_i = (s_{1i}, s_{2i})$, and then models the detection probability of an individual as a decreasing function the further a detector's (i.e. camera station) distance is to the individual's activity centre (Efford 2004). SECR models assume that individuals occupy home ranges which are unobserved and that successive trapping occasions are independent of each other (Noss et al. 2012). A state model, which is a spatial point process that describes the geographic distribution of home range centres within the landscape, is combined with the observation model, which estimates the probability of capturing an individual at a given detector relative to the distance of that detector from the individual's activity centre (Borchers and Efford 2008; Edwards et al. 2018). As cameras function independently of each other, then capture by one camera is not mutually exclusive so that individuals can be captured by multiple cameras (Royle et al. 2009). It is then presumed that the encounter rate of an individual *i* at a camera trap *j*, λij, declines as the distance from the home range centre increases, following a detection function, in this case a half-normal detection function. In a best-case scenario, where cameras are continuously operational and individual capture rates are independent in time, an individual may be captured a random number of times yielding encounter frequencies y_{ijk} for individual *i*, in trap *j*, during interval *k* with λ_0 as the baseline capture and g_{ij} is a function of distance between individual *i* and camera trap *j:*

$$y_{ijk} \sim Poisson(\lambda_0 g_{ij})$$

Thus, for a trap to be located at the exact individual's activity centre, λ_0 is the expected number of captures for that trap (Royle et al. 2009). The incorporation of trap locations into the analysis of SECR helps to recognise individual heterogeneity in capture probabilities and movement patterns (Sollmann et al. 2011; Bohm and Hofer 2018) and reduce the reliance on *ad hoc* buffer estimates to calculate density (Borchers 2012).

Using 'secr', I explored the most appropriate buffer size around the sampled area by varying buffer sizes from 10 up to 20 km until the models converged and determined a final buffer size of 10 km to be used for computations in 'secr' and 'SPACECAP'. This 10 km buffer was used to create a habitat mask around the trapping polygon to ensure the inclusion of all individual activity centres that were exposed to the cameras (Borchers and Efford 2008).

Maximum-Likelihood SECR

There are three kinds of model parameters for full maximum-likelihood SECR models: one is for density, one is for the probability of detecting an individual at the centre of its activity centre, or detection function g*0*, and one is for the spatial scale parameter σ, which is related to the average home range radius (Efford 2019). The σ is estimated based on information about animal movement provided by individuals that were captured at more the one camera trap station. I used the commonly adopted detection, the half-normal detection function in which the detection probability g_{ij} of individual *i* at station *j* during a sampling interval was estimated as

$$\hat{g}ij = \hat{g}_0 exp\left(\frac{-d^2{}_{ij}}{2\hat{\sigma}^2}\right)$$

where d_{ij} is the distance between the activity centre *i* and detector *j.* Parameter g_0 represents an individual's detection probability at its activity centre and σ represents the detection probability decay as a function of distance from its activity centre (Efford et al. 2011).

In 'secr', I fit models in which g*0* and σ were either constant or varying with covariates. The detection sub-models included models following the distance-based formulation described above, as well as detection functions that allowed g_0 and σ to vary in relation to covariates (Royle et al. 2013; Clare et al. 2015). Ithala Game Reserve is comprised of seven vegetation types (Figure 6). Camera trap stations were placed within four different vegetation types: Swaziland sour bushveld, Ithala quartzite sourveld, Paulpietersburg moist grassland and Northern Zululand sourveld. These vegetation types were implemented as camera-specific covariates such that the detection function parameters for an individual *i* at camera *j* were respectively estimated as $logit\,(\hat{g}_0) = \hat{\beta}_0 + \hat{\beta}_1 X_{1j} \ldots \hat{\beta}_n X_{nj}$ and $ln\,(\hat{\sigma}) = \hat{\beta}_0 + = \hat{\beta}_1 X_{1j} \ldots \hat{\beta}_n X_{nj}$. This formulation suggests that individuals will have different detection functions in relation to the attributes of specific camera locations (Efford 2012). Servals are considered to be grassland and savannah wetland specialists (Geertsema 1985; Bowland and Perrin 1993; Thiel 2011; Ramesh and Downs 2015a; Edwards et al. 2018), thus I varied g*0* and σ according to the vegetation type at each camera station. I fit the models where vegetation type varied with both g*0* and σ, with g*0* constant and σ only varying with vegetation and with g*0* varying with vegetation type and σ constant. Models were ranked based on Akaike's Information Criterion corrected for small sample size (AICc) (Hurvich and Tsai 1989).

Servals are known to be very elusive and difficult to see from a safari or general tourist vehicles. To test if servals avoid areas with higher vehicle traffic such as main reserve roads versus management tracks which receive very little vehicular traffic, I tested the model using vehicles as a detection factor. I calculated the mean number of vehicles per day passing by each camera trap station and allowed for g*0* to differ based on the vehicle activity at each station. Models were ranked based on AICc values and weights. The top models were further compared using a likelihood ratio test to determine the best fit. By referencing the time stamps on the camera trap images, temporal serval activity patterns were also compared to vehicle activity to further investigate the effects vehicles have on servals.

Bayesian SECR

For the Bayesian approach, the R package 'SPACECAP' 1.1.0 (Gopalaswamy et al. 2012a) was used. 'SPACECAP' specifies the same model as was carried out in 'secr' using the Markov chain Monte Carlo (MCMC) algorithm (Gardner et al. 2009; Royle et al. 2009; Singh et al. 2010; Noss et al. 2012). 'SPACECAP' also requires three input files: the capture histories of each individual serval, the trap deployment file combined with the camera activity information, along with the state space file detailing the surveyed area containing the camera traps and extended buffer that represents potential animal activity centres. I selected the Bernoulli distribution with trap response absent and a half normal detection function. The data augmentation, which supplements the dataset of known individuals with an arbitrarily large dataset of zero-detected histories (Noss et al. 2012), was set from 5 to 30 times the number of individual servals captured in each survey and the number of MCMC iterations and burn-in period were gradually increased until model convergence was reached for each model. Convergence was checked by examining Geweke diagnostics (*Z* scores, Geweke 1992), if the *Z* score value is between -1.6 and 1.6, then convergence has been achieved (Gopalaswamy et al. 2012b). The Bayesian *p* value produced by 'SPACECAP' shows model adequacy, with inadequacy when *p* values are close to 0 or 1 and adequacy when values are close to 0.5.

4. Results

2019 Serval Array

An additional 20 camera trap stations were added to the original Panthera leopard array to generate the serval camera trapping array. These stations were active simultaneously with the leopard array and were active for a total of 52 days of camera trapping with 49 dual camera stations resulting in trapping effort over the course of the entire study of 4 862 trap nights and a trapping array of 180.34 km^2. The total number of photographs was 12 272 and consisted of 10 087 photos of mammals. Throughout the survey, 46 mammal species were photographed including 16 carnivore species, among which four were large carnivores (leopard, brown hyena, spotted hyena, African wild dog). Leopard remained the most commonly photographed carnivore with an average trap success of 6.41 captures per 100 trap night. Naïve occupancy was calculated for all species captured and ranged from 0.02 for aardwolf (*Proteles cristata*), dwarf mongoose (*Helogale parvula),* hippopotamus (*Hippopotamus amphibious*), klipspringer (*Oreotragus oreotragus*) and Natal red rock rabbit (*Pronolagus crassicaudatus*) up to 1.00 for greater kudu (*Tragelaphus strepsiceros*) and human (*homo sapien)* (see Figure 9 and Table 3).

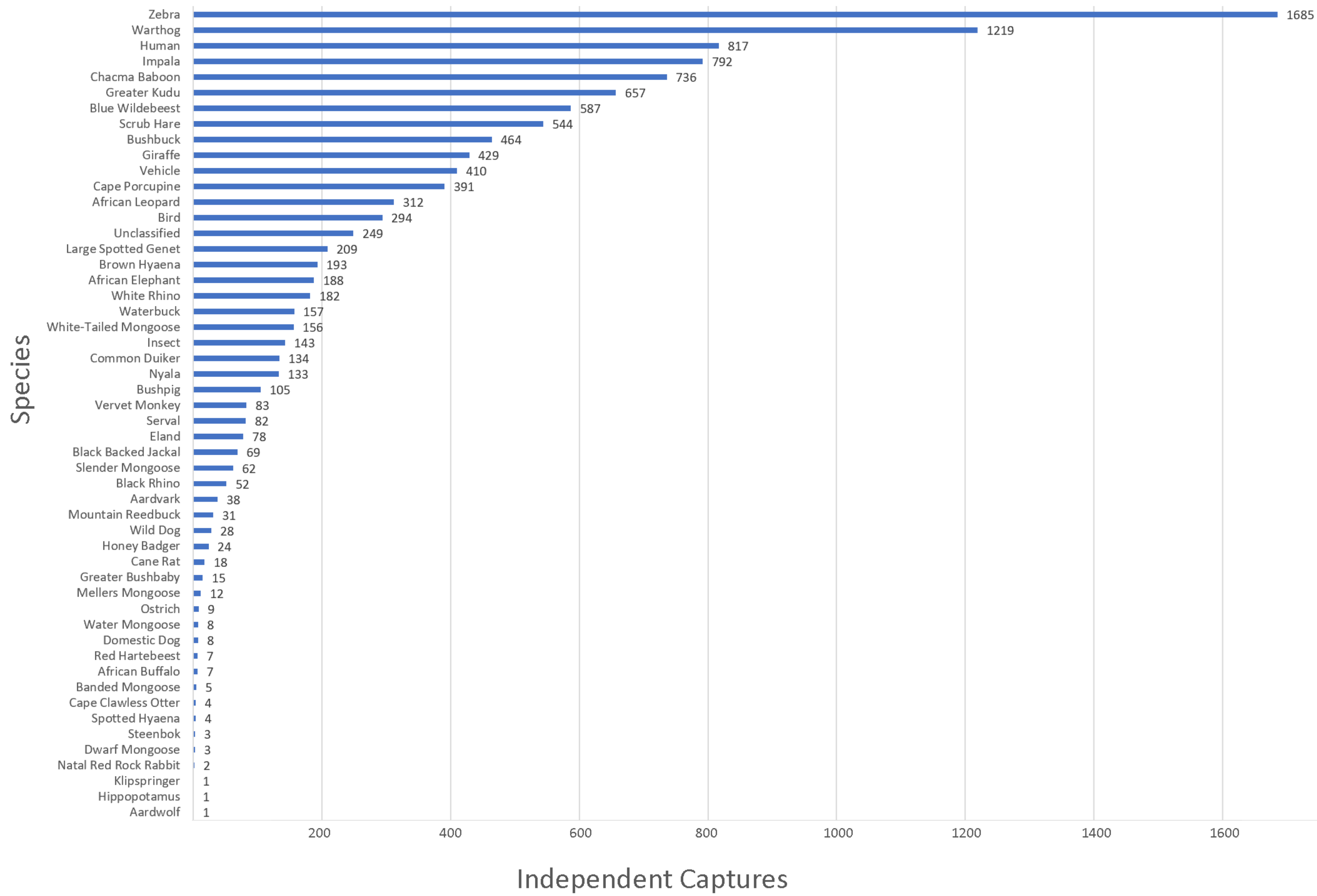

Figure 8. Number of photographic capture events by species for the serval array.

Table 3. Naïve occupancy, the proportion of sites that recorded at least one photograph of the target species, by species photographed in the 2019 serval array at Ithala Game Reserve, South Africa.

Species	Common name	Naïve occupancy
Carnivora		
Aonyx capensis	Cape Clawless Otter	0.08
Atilax paludinosus	Water Mongoose	0.12
Canis mesomelas	Black-backed Jackal	0.29
Crocuta crocuta	Spotted Hyena	0.08
Leptailurus serval	Serval	0.35
Galerella sanguinea	Slender Mongoose	0.35
Genetta tigrina	Large-spotted Genet	0.84
Helogale parvula	Dwarf Mongoose	0.02
Hyaena brunnea	Brown Hyena	0.80
Ichneumia albicauda	White-Tailed	0.71
Lycaon pictus	Wild Dog	0.33
Mellivora capensis	Honey Badger	0.29
Mungos mungo	Banded Mongoose	0.10
Panthera pardus	Leopard	0.92
Proteles cristata	Aardwolf	0.02
Rhynchogale melleri	Meller's Mongoose	0.10
Lagomorpha		
Lepus saxatalis	Scrub Hare	0.57
Pronolagus crassicaudatus	Natal red rock rabbit	0.02
Perissodactyla		
Ceratotherium simum	White Rhinoceros	0.82
Diceros bicornis	Black Rhinoceros	0.47
Equus quagga	Plains Zebra	0.96
Primates		
Cercopithecus pygerythus	Vervet Monkey	0.39
Otolemur crassicaudatus	Greater Bushbaby	0.08
Papio ursinus	Chacma Baboon	0.96
Proboscidae		
Loxodonta africana	African Elephant	0.78
Rodentia		
Hystrix africaeaustralis	Cape Porcupine	0.84
Thryonomys swinderianus	Cane Rat	0.20

Table 6. (continued)

Species	Common name	Naïve occupancy
Ruminantia		
Aepyceros melampus	Impala	0.88
Alcelaphus buselaphus	Red Hartebeest	0.08
Connochaetes taurinus	Blue Wildebeest	0.76
Giraffa camelopardalis	Giraffe	0.86
Kobus ellipsiprymnus	Waterbuck	0.59
Oreatragus oreotragus	Klipspringer	0.02
Ruminantia		
Potamochoerus porcus	Bushpig	0.71
Raphicerus campestris	Steenbok	0.06
Redunca fulvorufla	Mountain Reedbuck	0.18
Ruminantia		
Sylvicapra grimmia	Common Duiker	0.57
Syncerus caffer	African Buffalo	0.06
Taurotragus oryx	Eland	0.51
Tragelaphus angasii	Nyala	0.45
Tragelaphus scriptus	Bushbuck	0.69
Tragelaphus strepsiceros	Greater Kudu	1.00
Suiformes		
Hippopotamus amphibious	Hippopotamus	0.02
Phacochoerus africanus	Warthog	0.78
Tubulidentata		
Orycteropus afer	Aardvark	0.43
Domestic		
Canis familiaris	Dog	0.12
Human		
Homo sapien	Human	1.00
	Vehicle	0.94
Other		
	Bird species	0.86
	Insect species	0.63

Servals were photographed a total of 151 times, of which 82 were independent capture events at 16 trap stations. This resulted in a capture rate of 1.69 independent captures per 100 trap nights. 137 (87.3%) photos were suitable for individual identification. Simultaneous photographs of both the left and right flank were available for eight individuals. Of those individuals, one was a kitten and excluded from analyses. Three individuals were photographed on their left side only, and five individuals were photographed on their right flank only. Due to the higher number of individuals from right flank, the three individuals that were only identifiable from the left side were excluded from model inputs to avoid inflating the population estimate and only right flank, together with those individuals for which we had both flanks were used in the final analyses. Nine capture events in which individuals could not be identified were excluded from the analyses. The final number of individually identifiable individuals was 12 derived from with 69 independent capture events at 16 trap stations. The number of independent captures per individual ranged from 1 to 26. Nine individuals were recaptured a total of 67 recapture events. There were 7 spatial recaptures over 27 spatial recaptures events. Three servals were photographed only once whereas nine individuals were recaptured up to 26 times each. One individual was captured at 11 stations, two at three stations, five at two stations, and four were only photographed at one station. One station had five individuals captured at it and another station had three individuals captured with a total of 20 independent captures.

Maximum Likelihood Based SECR

Using the package 'secr' in R, I determined the size of suitable habitat within the area containing the trapping polygon and 10 km buffer to be 1 066 km^2. The top model was fitted with a half normal detection function, and the mean density was 2.49 ± 0.8 individuals/100 km^2 (Table 7).

Table 7. Population size and density estimates for servals in Ithala Game Reserve based on maximum likelihood SECR models for the serval array.

Model	g_0 Mean ± SE	σ (m) Mean ± SE	$\hat{N}$ Mean ± SE	D Mean ± SE	AICc
g_0~[.] σ ~[.]	0.01 ± 0.005	2363 ± 313	27 ± 8.6	2.49 ± 0.8	716.78

$\hat{N}$, population size; D, serval density (individuals/100 km2); [.], parameter constant; g0, detection probability; ML, maximum likelihood; g_0, expected encounter frequency at trap location considered as home range centre; σ, spatial scale parameter; AICc, Akaike's Information Criterion corrected for small sample size.

Bayesian Based SECR

In 'SPACECAP', I ran 80 000 iterations, of which the initial 10 000 were discarded as the burn-in period. I used a thinning rate of five and specified an augmentation value of 200 individuals, which was assumed to be well above the expected number of individuals. The Geweke's diagnostic score showed that the model had converged with a reported Bayesian *p* value of 0.83. Although the Bayes P value suggests poor model fit (ideally it should be between 0.25 and 0.75), the posterior density graphs of all parameters outputted by ''SPACECAP'' suggest that the model results are reliable. Mean density was estimated at 2.54 ± 0.7 individuals/100 km^2 (Table 8).

Table 8. Posterior summary statistics and Z scores from 'SPACECAP' analysis performed on serval within Ithala Game Reserve

Parameter	Posterior mean	Posterior *SD*	95% lower HPD level	95% upper HPD level	*Z* score
Sigma[a]	2.45e+03	3.52e+02	1.83e+03	3.16e+03	-0.4454
Lam0[b]	2.21e-02	4.62e-03	1.38e-02	3.15e-02	-0.1548
Psi[c]	1.33e-01	4.13e-02	6.14e-02	2.18e-01	0.9583
Nsuper[d]	2.73e+01	7.36e+00	1.40e+01	4.10e+01	0.7099
Density[e]	2.54e-02	6.84e-03	1.40e-02	3.91e-02	

[a]Spatial-scale parameter over which detection declines. [b]probability of capture at the centre of an individual's home range. [c]data augmentation parameter. [d]Population size of individuals having their activity centres within the effective trapping area. [e]serval/100 km2.

2019 Leopard Array

The Panthera leopard array, which ran simultaneously with the serval array, was active for a total of 52 days with 29 dual camera stations. This resulted in 2 911 trap nights with a total of 7 433 independent photographs, 6 113 of which were of mammals. Throughout the survey, 46 mammal species were photographed including 16 carnivore species, among which four were large carnivores (leopard, brown hyena, spotted hyena, African wild dog). The most commonly photographed carnivore was leopard with a mean trap success of 6.45 captures per 100 trap nights. Naïve occupancy was calculated for all species captured and ranged from 0.03 for dwarf mongoose (*Helogale parvula*) and Natal red rock rabbit (*Pronolagus crassicaudatus*) up to 1.00 for greater kudu (*Tragelaphus strepsiceros*) and human (*Homo sapien)* (see Figure 8 and Table 4).

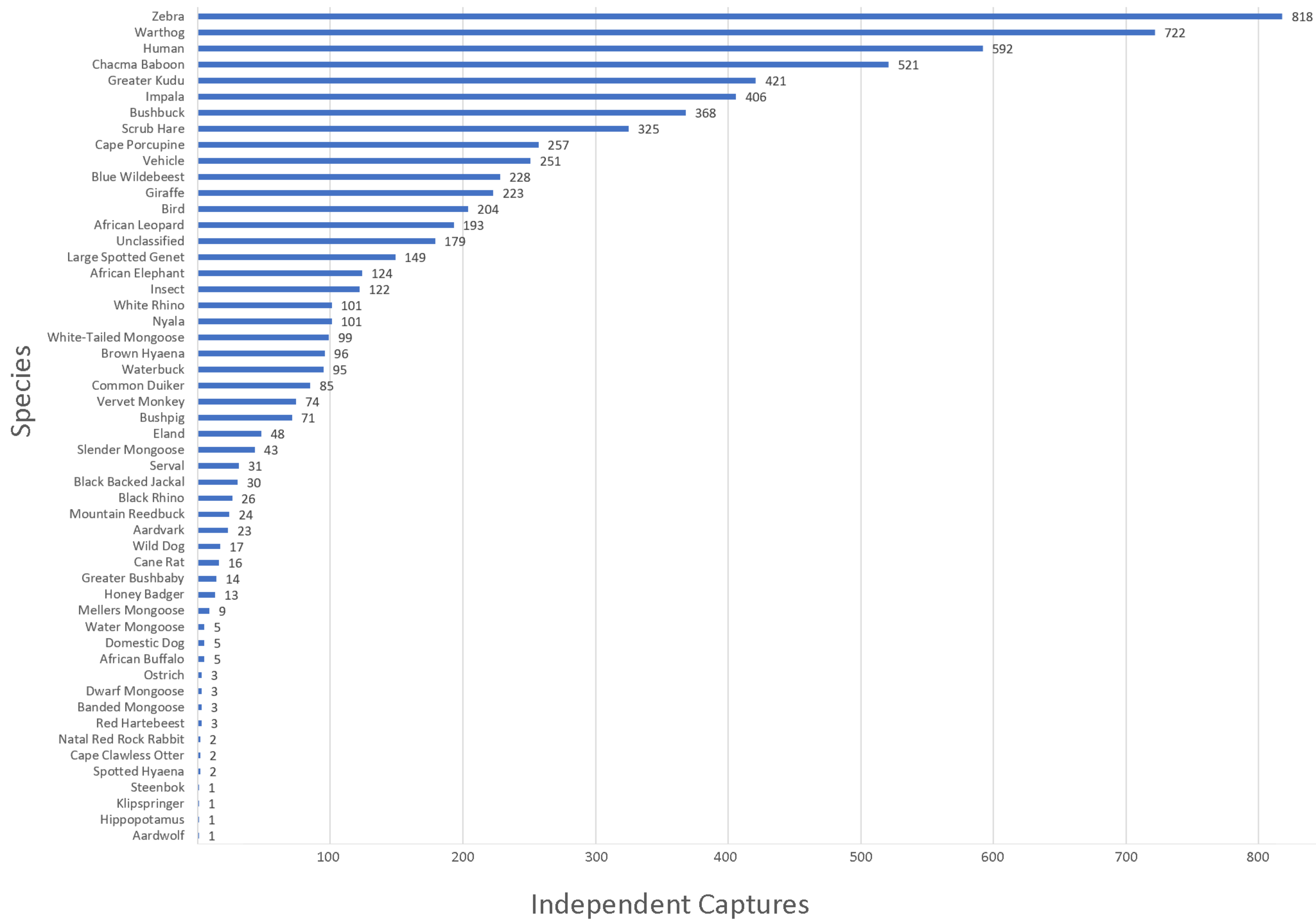

Figure 9. Number of independent photographic capture events for all species detected on the leopard camera trap array.

Table 4. Naïve occupancy, the proportion of sites that recorded at least one photograph of the target species, by species photographed in the 2019 leopard array at Ithala Game Reserve, South Africa.

Species	Common name	Naïve occupancy
Carnivora		
Aonyx capensis	Cape Clawless Otter	0.07
Atilax paludinosus	Water Mongoose	0.10
Canis mesomelas	Black-backed Jackal	0.21
Crocuta crocuta	Spotted Hyena	0.07
Leptailurus serval	Serval	0.31
Galerella sanguinea	Slender Mongoose	0.28
Genetta tigrina	Large-spotted Genet	0.83
Helogale parvula	Dwarf Mongoose	0.03
Hyaena brunnea	Brown Hyena	0.72
Ichneumia albicauda	White-Tailed Mongoose	0.66
Lycaon pictus	Wild Dog	0.31
Mellivora capensis	Honey Badger	0.28
Mungos mungo	Banded Mongoose	0.10
Panthera pardus	Leopard	0.86
Proteles cristata	Aardwolf	0.03
Rhynchogale melleri	Meller's Mongoose	0.14
Lagomorpha		
Lepus saxatalis	Scrub Hare	0.52
Pronolagus crassicaudatus	Natal red rock rabbit	0.03
Perissodactyla		
Ceratotherium simum	White Rhinoceros	0.79
Diceros bicornis	Black Rhinoceros	0.38
Equus quagga	Plains Zebra	0.93
Primates		
Cercopithecus pygerythus	Vervet Monkey	0.45
Otolemur crassicaudatus	Greater Bushbaby	0.10
Papio ursinus	Chacma Baboon	0.93
Proboscidae		
Loxodonta africana	African Elephant	0.72
Rodentia		
Hystrix africaeaustralis	Cape Porcupine	0.83
Thryonomys swinderianus	Cane Rat	0.28
Ruminantia		
Aepyceros melampus	Impala	0.93

Table 3. (continued)

Species	Common name	Naïve occupancy
Ruminantia		
Alcelaphus buselaphus	Red Hartebeest	0.07
Connochaetes taurinus	Blue Wildebeest	0.66
Giraffa camelopardalis	Giraffe	0.79
Kobus ellipsiprymnus	Waterbuck	0.59
Oreatragus oreotragus	Klipspringer	0.03
Ruminantia		
Potamochoerus porcus	Bushpig	0.79
Raphicerus campestris	Steenbok	0.03
Redunca fulvorufla	Mountain Reedbuck	0.14
Ruminantia		
Sylvicapra grimmia	Common Duiker	0.59
Syncerus caffer	African Buffalo	0.03
Taurotragus oryx	Eland	0.55
Tragelaphus angasii	Nyala	0.52
Tragelaphus scriptus	Bushbuck	0.76
Tragelaphus strepsiceros	Greater Kudu	1.00
Suiformes		
Hippopotamus amphibious	Hippopotamus	0.03
Phacochoerus africanus	Warthog	0.76
Tubulidentata		
Orycteropus afer	Aardvark	0.52
Domestic		
Canis familiaris	Dog	0.14
Human		
Homo sapien	Human	1.00
	Vehicle	0.90
Other		
	Bird species	0.90
	Insect species	0.72

Servals were photographed a total of 49 times, of which 31 were independent capture events (camera trap captures with a time interval greater than one hour) at nine trap stations. This resulted in a capture rate of 1.04 independent captures per 100 trap nights. 43 (86%) photos were suitable for individual identification. Simultaneous photographs of both the left and right flank were available for six individuals. Two individuals were photographed on their left side only, and three individuals were photographed on their right flank only. The two individuals that were only identifiable from the left side were thus excluded from model inputs. Three capture events in which individuals could not be identified were also excluded from the analyses. The final number of individually identifiable servals was ten individuals derived from 25 independent capture events at nine trap stations. The number of independent captures per individual ranged from one to eight. Five individuals were recaptured a total of 20 recapture events. There were four spatial recaptures over 14 spatial recapture events. One individual was captured at five stations, one at three stations, three at two stations, and five were only photographed at one station.

Maximum Likelihood Based SECR

Using ML-based SECR, the size of suitable habitat within the area containing the trapping polygon and 10 km buffer was 1066.31 km^2. The mean density was 1.73 ± 0.8 individuals/100 km^2 (Table 4).

Table 4. Population size and density estimates for servals in Ithala Game Reserve based on maximum likelihood SECR models for the leopard array.

Model	g_0 Mean ± SE	σ (m) Mean ± SE	N̂ Mean ± SE	D Mean ± SE	AICc
g_0~[.] σ ~[.]	0.03 ± 0.006	3095 ± 678	18 ± 8.18	1.73 ± 0.8	251.81

N̂, population size; D, serval density (individuals/100 km2); [.], parameter constant; g0, detection probability; ML, maximum likelihood; g_0, expected encounter frequency at trap location considered as home range centre; σ, spatial scale parameter; AICc, Akaike's Information Criterion corrected for small sample size.

Bayesian SECR

In 'SPACECAP', I ran 80 000 iterations, of which the initial 10 000 were discarded as the burn-in period. I used a thinning rate of five and specified an augmentation value of 200 individuals, which was assumed to be well above the expected number of individuals. A Bayesian *p* value of 0.58 was estimated, which suggested good model fit. Serval density was estimated at 2.45 ± 0.89 individuals/100 km^2 (Table 5).

Table 5. Posterior summary statistics and Z scores from program 'SPACECAP' for serval within Ithala Game Reserve.

Parameter	Posterior mean	Posterior *SD*	95% lower HPD level	95% upper HPD level	*Z* score
Sigma[a]	2.540e+03	6.04e+02	1.61e+03	3.76e+03	**-0.5724**
Lam0[b]	1.49e-02	6.64e-03	4.56e-03	2.85e-02	**1.3857**
Psi[c]	1.30e-01	5.14e-02	4.58e-02	2.34e-01	**0.1147**
Nsuper[d]	2.63e+01	9.59e+00	1.10e+01	4.50e+01	**-0.1501**
Density[e]	2.45e-02	8.92e-03	1.02e-02	4.19e-02	

[a]Spatial-scale parameter over which detection declines. [b]probability of capture at the centre of an individual's home range. [c]data augmentation parameter. [d]Population size of individuals having their activity centres within the effective trapping area. [e]serval/100 km2.

Comparison of camera trap deployments

The serval array added 20 additional camera trap stations to the 29 original stations from the leopard array (Figure 10). This resulted in servals being captured at 16 different stations in the total serval array and nine different stations in the leopard array (Table 9).

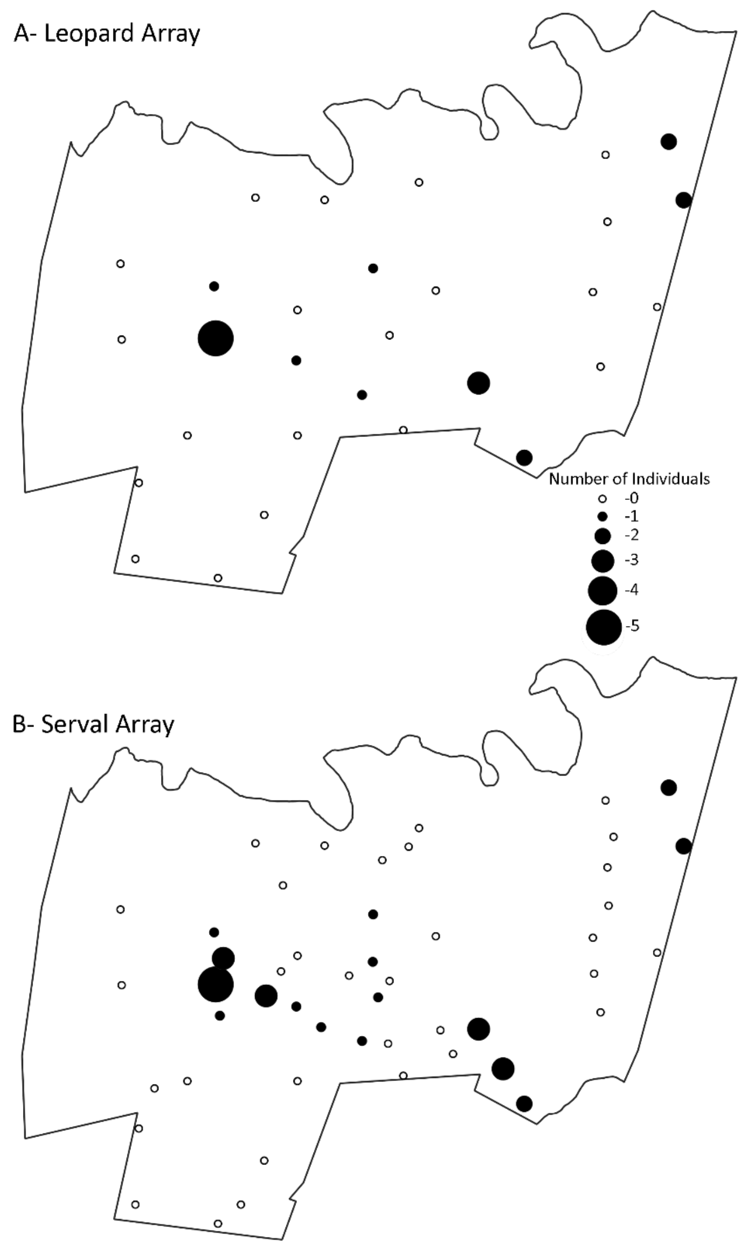

Figure 10. Number of individual servals recorded at camera trap stations in Ithala Game Reserve, South Africa during the 2019 survey with the A-leopard array compared to the B-serval array. Larger circles indicate a larger number of serval captures.

Table 5. Comparison of the Panthera leopard camera trapping array with the 2019 serval array at Ithala Game Reserve, South Africa.

Variable	Leopard Array	Serval Array
No. camera trap stations	30	49
No. camera trap nights	2 911	4 862
No. stations detecting serval	9	16
No. of independent serval captures	30	78
No. individual serval	10	12
No. of recaptures	5	9
No. spatial recaptures	4	7

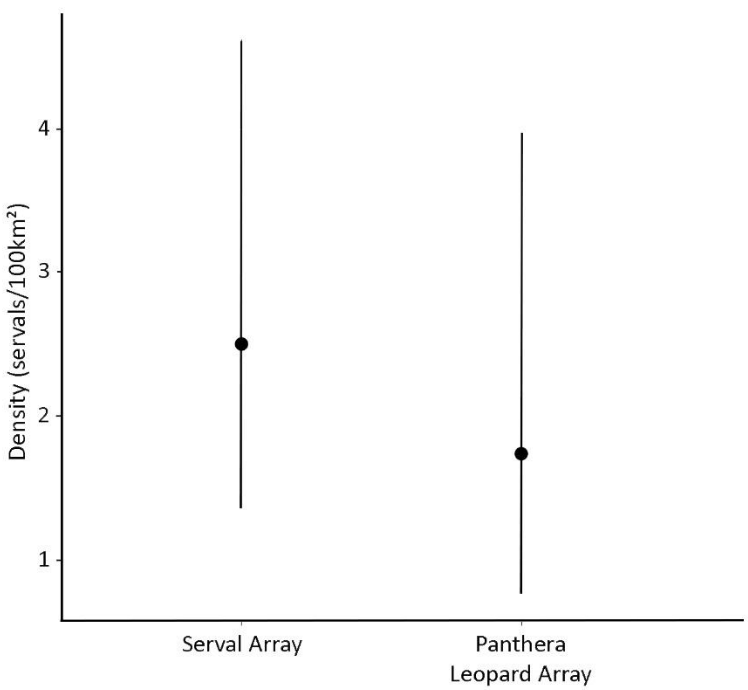

Figure 11. Comparison of serval density estimates, including upper and lower confidence levels, for the serval and leopard specific camera trap arrays at Ithala Game Reserve, South Africa in 2019.

Table 6. Population size and density estimates for servals in Ithala Game Reserve based on maximum likelihood SECR models.

Survey	Model	g_0 Mean ± SE	σ (m) Mean ± SE	N̂ Mean ± SE	D Mean ± SE
Leopard Array	g_0~[.] σ ~[.]	0.03 ± 0.006	3095 ± 678	18 ± 8.18	1.73 ± 0.8
Serval Array	g_0~[.] σ ~[.]	0.01 ± 0.005	2363 ± 313	27 ± 8.6	2.49 ± 0.8

N̂, population size; D, serval density (individuals/100 km2); [.], parameter constant; g0, detection probability; ML, maximum likelihood; g_0, expected encounter frequency at trap location considered as home range centre; σ, spatial scale parameter.

Model Parameters

Models were ranked based on AICc values and weights and showed that vehicle activity had little to no significant impact on serval densities at Ithala (Table 7). SECR models ranked higher when the vehicle activity and vegetation covariates were excluded.

Table 7. Log-likelihood, AIC, AICc, dAICc and AICc weight for models ran in 'secr' for different parameters of serval density estimates.

Model	Parameters	Log Likelihood	AIC	AICc	dAICc	AICcwt
g_0~[.] σ ~[.]	3	-375.618	757.236	760.664	0	0.8095
g_0~Vehicles σ ~[.]	4	-374.445	756.891	763.558	2.894	0.1905
g_0~Veg σ ~[.]	6	-373.559	759.117	780.117	19.453	0
g_0~[.] σ ~Veg	6	-375.279	762.558	783.558	22.894	0
g_0~Veg σ ~Veg	9	-369.189	756.377	936.377	175.713	0

AICc, Akaike's Information Criterion corrected for small sample size; AICcwt, weight of support for each model; dAICc, difference in model weight; g_0, detection probability; r, spatial scale parameter; [.], parameter constant; Vehicles; mean vehicle activity; Veg, vegetation type.

A comparison of the null model with the model with g*0* varying with the mean number of vehicles per day using the likelihood ratio test resulted in a chi square result of 2.3448, degrees of freedom of 1 and a p-value of 0.126.

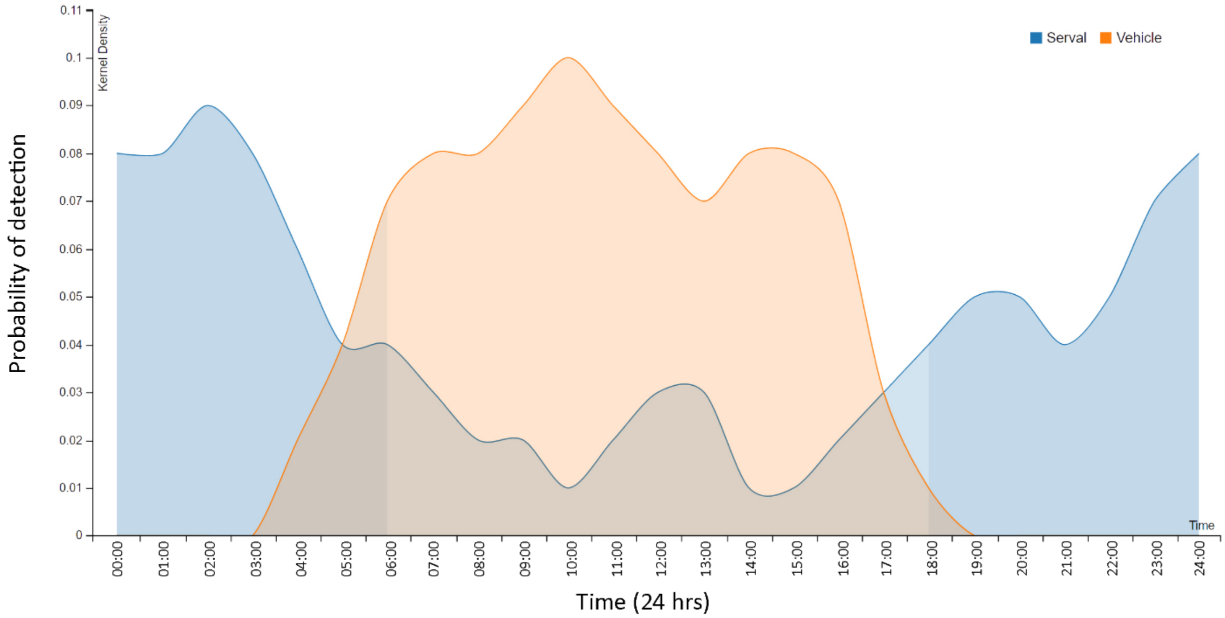

Figure 12. Activity patterns of servals and vehicle activity during the 2019 survey at Ithala Game Reserve, South Africa.

Ithala Serval Density Estimates using the leopard survey data from 2013 to 2019

Since 2013, serval densities at Ithala Game Reserve have fluctuated from a low of 1.42 individuals/100 km² in 2018 to 9.66 individuals/100 km² in 2014 (Table 12). Survey dates did fluctuate from year to year. The 2013, 2014, 2016 and 2017 surveys all took place during the drier winter months while the 2015, 2018 and 2019 surveys took place during the wetter summer months.

Table 8. Serval density estimates at Ithala Game Reserve, South Africa from 2013 to 2019.

Year	Survey Dates	Seasonal Rain	Trap Days	No. of Stations	No. Captures	No. Individuals	No. of Recaptures	Density	Density ± SD	σ (m) meters
2013	27 Aug-10 Oct (44 days)	0-50 mm	1545	36	34	17	8	5.33(ML) 5.9(Bayes)	1.5 1.6	2084 2170
2014	29 Jun-12 Aug (44 days)	0-50 mm	1340	31	55	27	12	9.66(ML) 10.6(Bayes)	2.1 2.2	1570 1600
2015	29 Mar-12 May (44 days)	500-2,000 mm	1349	31	23	12	4	3.39(ML) 3.7(Bayes)	1.3 1.6	3090 3810
2016	24 Jul-5 Sep (43 days)	0-50 mm	1345	29	57	13	8	5.33(ML) 6.0(Bayes)	1.6 1.6	1046 1180
2017	24 Jul-14 Sep (52 days)	0-50 mm	1479	30	34	9	6	2.27(ML) 2.61(Bayes)	0.8 0.8	2058 2110
2018	29 Jan-22 Mar (53 days)	300-500 mm	1455	30	21	6	4	1.42(ML) 1.67(Bayes)	0.6 0.6	2309 2460
2019[a]	2 Feb-2 Apr (60 days)	500-2,000 mm	2911	29	19	10	9	1.73(ML) 2.45(Bayes)	0.8 0.9	3095 2450
2019[b]	2 Feb-2 Apr (60 days)	500-2,000 mm	4862	49	63	12	5	2.49(ML) 2.54(Bayes)	0.8 0.7	2363 2410

[a]2019 leopard camera trap array, [b]2019 serval camera trap array

Figure 13. The number of individual servals recorded at camera trap stations in Ithala Game Reserve, South Africa during the 2013-2019 Panthera leopard camera trap surveys.

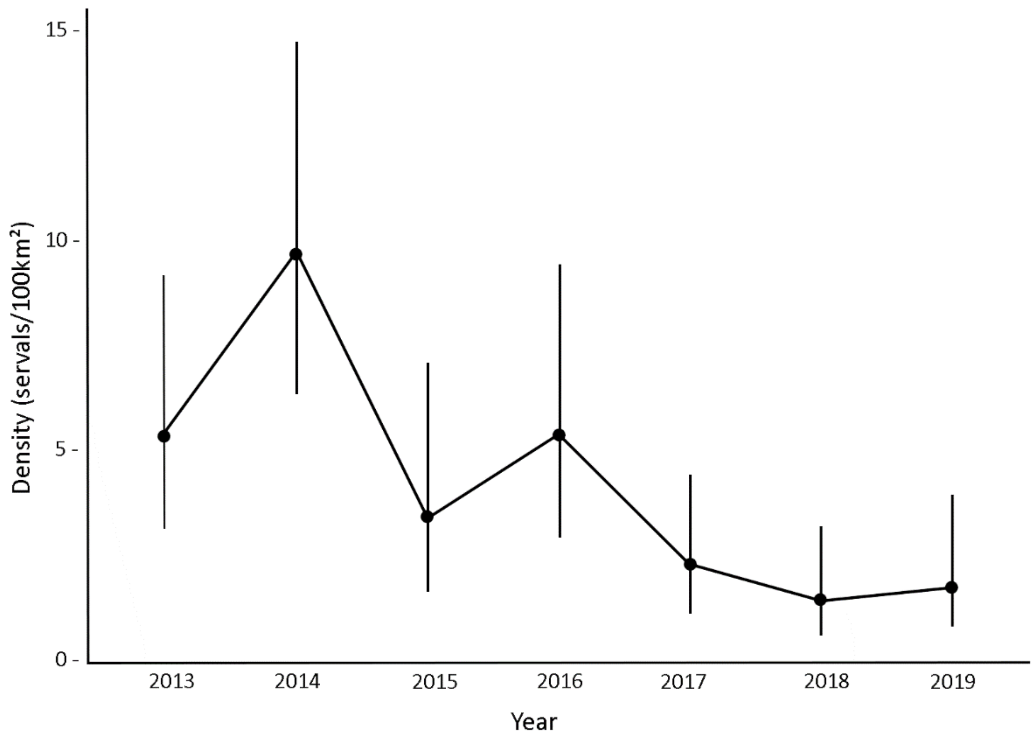

Figure 14. Serval population density estimates, including upper and lower confidence levels, for Ithala Game Reserve, South Africa from 2013 to 2019 from Panthera Leopard Survey data.

Leopard density estimates from Ithala dropped from 8.9 ± 1.7 leopards/100 km^2 in 2018 down to 3.8 ± 0.9 leopards/100 km^2 in the 2019 survey.

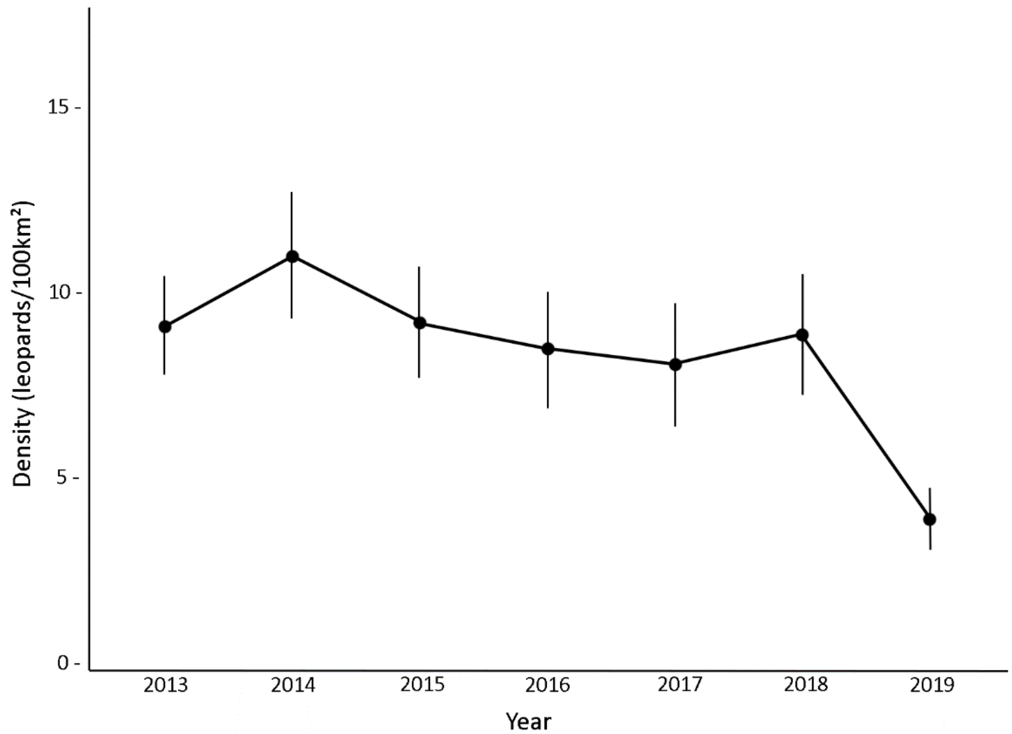

Figure 15. Leopard population density estimates, including upper and lower confidence levels, for Ithala Game Reserve, South Africa from 2013 to 2019. Data provided by G.Mann (Panthera).

5. Discussion

The funding of routine population surveys to determine the population status of a range of wildlife species is a major challenge for wildlife management globally (Barrows *et al* 2005; Barea-Azcón et al. 2007). Currently most funding is raised for research on charismatic megafauna including large carnivores (Caro 2003; Ogada et al. 2003; Ray et al. 2005; Dalerum et al. 2008). As a consequence, mesocarnivore population research is lacking and is often based on by-catch from surveys funded and designed for large, charismatic predators. Density estimation is a key component of building ecological knowledge of a species and a key parameter of interest in conservation and management efforts (Sun et al. 2014). Density remains a difficult parameter to measure in natural systems particularly for wide ranging cryptic species (Kéry et al. 2011; Thiel 2011; Edwards et al. 2018). In this study I used data from a long-term leopard survey within a protected area to explore annual trends in serval density. Additionally, I used data obtained in the 2019 leopard survey to compare with data obtained from an intensified array designed more specifically for serval (reduced distance between camera trap stations and more effort in preferred serval habitat). The two surveys were compared to determine whether density estimates derived from a leopard survey are comparable with the serval array (i.e., similar means with overlapping confidence intervals) and how variation in effort and placement may influence the precision of the density estimates. This allowed me to assess the validity of using arrays designed for well-funded large charismatic predators to assess the density of smaller individually recognised carnivores like serval.

Comparing the leopard and serval arrays

Only two additional serval individuals were detected on the serval-specific array compared to the leopard-specific array. While higher capture rates were predicted for the serval array, the more important result was that the serval array had 47 more recaptures (67 versus 20) and 13 more spatial recaptures (27 versus 14) both of which are important for the accuracy of model output. Using maximum likelihood spatially explicit capture-recapture methods, serval density was estimated as 1.73 ± 0.77 (0.76-3.97) individuals/100 km² for the leopard array and 2.49 ± 0.81 (1.24-4.63) individuals/100 km² for the serval array in Ithala Game Reserve in 2019. However, the 95% confidence intervals of both estimates were relatively broad and overlapped with one another (see Figure 11). I found that density estimates derived from a serval-specific array were similar to those derived from the leopard array, but that both lacked precision and hence confidence in the estimate. Foster and Harmsen (2012) showed that small sample sizes, study area size and low capture probabilities are all potential problems with density studies based on camera trap data and may lead to imprecision (Sollmann et al. 2012). In this study, low capture probabilities, likely linked to small population size, are likely to be the main reason for the large error in the density estimates for both surveys. The lower estimate for the leopard survey is thus a function of the greater camera trap spacing on this array with larger distances between camera traps allowing for smaller species (with smaller home ranges) to persist in the space between sampling points lowering the probability of detection and resulting in fewer spatial recaptures (Sollmann et al. 2014; Sun et al. 2014; Rocha et al. 2016) and a poorly estimated movement parameter, σ (Tobler and Powell 2013; Rocha et al. 2016). From 2013-2019, the Panthera leopard surveys at Ithala Game Reserve took place during different seasons. The 2013, 2014, 2016 and 2017 surveys took place during the dry season with average rainfall of 0-50 mm while the 2015, 2018 and 2019 surveys took place during the wet season with average rainfall in the 300-2 000 mm range. Byrom et al. (2018) reported that there was a positive relationship between rainfall in the wet season with small mammal abundance followed by a peak in rodent-eating carnivores 6-12 months after the small mammal peak. Inconsistent seasonal timing of the surveys could have led to inconsistent trends in serval densities. Although the seasons varied by survey year, there does not appear to be a correlated fluxation in σ (see Figure 12).

There is little published data on home rang size within protected areas for serval and hence no clear guideline on the minimum survey effort required for generating accurate serval density estimates. The mean intertrap distance between my cameras in the serval array was conservative compared to the spacing used in other serval density studies using SECR models (see Table 1). My model output figures for σ are similar to other serval studies (Kane et al. 2014; Bohm and

Hofer 2018; Edwards et al. 2018) and while σ was lower for the serval array than for the leopard array (3088 ± 313 versus 5513 ± 679), it was still higher than the σ reported by Ramesh and Downs (2013b) for serval in the Drakensberg Midlands.

Petersen et al. (2019) suggested that leopard cat (*Prionailurus bengalensis)* movements may be greater when resources are scarce and that this would reflect in an increase in ranging behaviour (Fuller and Sievert 2001), and thus larger σ outputs. Micromammals are inadequately sampled by camera trap surveys and given their importance to serval diet it was not possible to assess the effects of food availability on ranging behaviour in the study population. The greater cane rat (*Thryonomys swinderianus*) is the only medium sized rodent that was regularly detected on the camera traps (0.37 captures/100 trap nights), but neither estimates of density or abundance were possible using the survey design. However, a plot of serval activity patterns together with those of cane rats does suggest that activity patterns may overlap both spatially and temporarily and further research on prey availability across years might help explain annual trends moving forward (Figure 16).

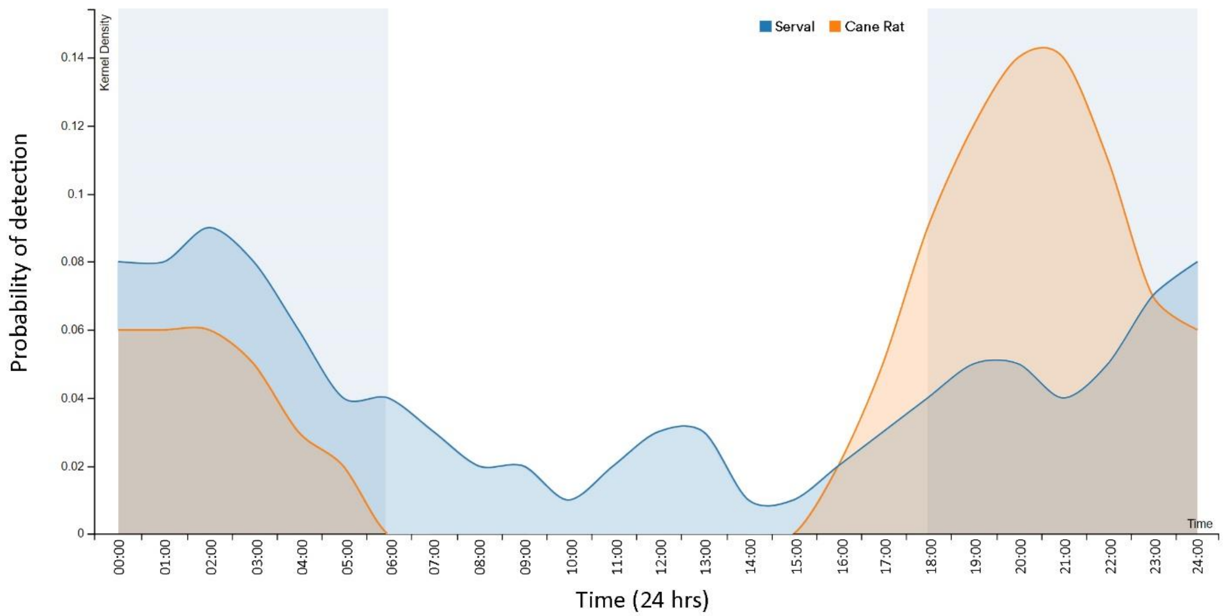

Figure 16. Activity patterns of servals and cane rats in Ithala Game Reserve derived from the time stamp of detections of both species on the serval array in 2019. The blue shading refers to night-time and the white to daytime.

Panthera's leopard surveys across multiple protected areas in KwaZulu-Natal revealed that Ithala historically has had the highest serval densities and was thus an ideal site for this study. However, with serval density declining over time it may be necessary to extend the duration of future camera trap surveys (Weingarth et al. 2015). Tobler and Powell (2013b) recommended a survey length up to 120 days for improved precision when estimating densities of jaguar (*Panthera onca*), which occur naturally at low densities and have low detection probabilities. Karanth (1995) and Kwanishi and Sunquist (2004) sampled for 6-14 months to increase the number of captures of tigers. However, increasing the duration of surveys increases the likelihood of violating a key assumption of SECR models; namely demographic closure of the sampled population. True demographic closure is seldom assured even during short sample sessions; animals can immigrate or disappear at any time of year including during surveys. Clearly there are trade-offs between increasing capture probabilities and violating model assumptions (Otis et al. 1978; Rexstad and Burnham 1991), but consensus suggests running surveys for longer (Foster and

Harmsen 2012; Weingarth et al. 2015) and comparing model outputs with sequentially reduced survey duration. Implicit in this approach is the acceptance that the consequences of small sample sizes and sparse captures outweigh the risk of violating closure with longer session lengths (Harmsen et al. 2011; Noss et al. 2013; Tobler and Powell 2013). Weingarth (2015) acknowledges that new studies without species-specific information from the study site should not expect high trap success (<50%) within the first monitoring session.

Other potential limitations of my dataset include the absence of sex as a covariate. Bohm and Hofer (2018) suggested using sex as a covariate in maximum-likelihood spatially explicit capture-recapture models after finding that male and female servals had different activity patterns which they suggested may reflect avoidance of areas with high larger carnivore densities. Sollmann et al. (2011) found that that including sex as a covariate improved estimates for jaguar camera trap studies and that models excluding sex covariates can overestimate density by causing a negative basis in density estimates. My cameras only recorded one photo per trigger event, limiting my ability to discern subtle morphological differences between individuals that can be used to discern sex. Servals are not obviously sexually dimorphic and thus the detection of testes is the most reliable way to distinguish male from female. With only a single photograph per trigger, the probability of an image allowing for teste detection is low and while multiple photographs per trigger event might improve the chances of attributing sex this comes as a trade-off with depleted batteries and full SD cards without a guarantee of reliable sex determination. Only four out of a total of 12 individuals could be confidently sexed using the serval array – three males and one female with a kitten. I was thus not able to include sex as a covariate in the 'secr' models and to improve the precision of the density estimates.

To increase capture probability, and therefore the precision of my population density estimates, cameras were placed to maximise detection of individuals. Studies have shown that camera trap stations placed along roads and well-established game paths have higher potential of photographing many carnivore species (tigers, leopards, jaguars) as opposed to placing them in a random grid format (Karanth and Nichols 1998; Henschel and Ray 2003; Tobler and Powell

2013; Kane et al. 2014; Mann et al. 2014). Kane et al. (2014) conducted a pilot study where 80% of the cameras were placed on small animal trails and had no image captures of large nor medium sized carnivores on abandoned or slightly used trails. Placing cameras along roads and well-maintained paths, also made maintenance by vehicle or foot easier. Many of the additional serval grid cameras in my survey were placed in optimal habitat locations for capturing servals such as roads and paths going through open grassland where servals have been visually recorded in the past. Placing camera traps in locations of known serval habitat and along used pathways and roads instead of placing them randomly may explain the improved recaptures in the serval survey compared to the leopard survey. The 29 camera stations from the leopard array were also placed strategically in areas conducive to higher leopard use such as in drainage lines. Such placement might not favour serval to the same degree and together with lower effort may also explain the lower serval recaptures on the leopard survey.

Bayesian compared to maximum-likelihood SECR

Estimates produced by the Bayesian method, 'SPACECAP' were similar to those produced to ML SECR (Table 5). However, the Bayesian estimates were higher than 'secr' estimates, although the differences did not appear substantial. This trend is different to other studies and simulations which all reported lower estimates by 'SPACECAP' compared to 'secr' (Noss et al. 2012; Ramesh and Downs 2013; Bohm and Hofer 2018). In other surveys where data were sparse with too few captures and/or recaptures, 'secr' was more sensitive to this limitation than 'SPACECAP'. However, Noss et al. (2012) noted that in extreme cases of deficient data, 'SPACECAP' will continue to produce density estimates but the outputs confirm that the models do not achieve convergence while 'secr' will not produce estimates at all. My models did converge, but the low recaptures may have been a limiting factor and the explanation between the two estimates differing slightly.

Serval density estimates

The serval density estimates in my study are low compared to the 6.2 ± 1.9 serval/100 km^2 to 7.7 ± 1.6 serval/100 km^2 that Ramesh and Downs (2013b) recorded for farmlands in the Drakensberg Midlands of KwaZulu-Natal. The latter study took place in farmlands where domestic and naturally occurring wild ungulates occur together with medium and small carnivores but in the complete absence of large carnivores. While Ithala Game Reserve does not have lions, I did record leopards, brown hyenas, spotted hyenas and wild dogs in the survey all of which may prey on smaller carnivores such as serval (di Silvestre et al. 2000; Davies-Mostert et al. 2013; Ott et al. 2015). Just prior to the 2019 survey set up, the two wild dogs, which had not previously occupied Ithala, were seen on the reserve. During the camera trap survey, the wild dogs were captured on camera 56 times. While the occurrence of wild dogs on Ithala is recent, the new presence of a large carnivore might have disrupted normal serval movements during the survey.

Similar results of higher occupancy for medium-sized carnivores (e.g. jackal, caracal) on farmland compared to protected areas in KwaZulu-Natal (PAs) was reported by Pretorius (2019). In this study the combination of access to domestic livestock and the absence of larger predators was evoked to explain the higher mesopredator occupancy on farmland. It appears that similar processes may explain the differences between my results and those of Ramesh and Downs (2013b) with support from Bohm and Hofer (2018) who reported that female servals changed their activity patterns when spotted hyena densities were high. Higher serval density on farmland may reflect habitat modification linked to anthropogenic activities (e.g., crops) such that these environments provide access to larger rodent populations in addition to permanent artificial water sources. Increased resource availability, reduced predation pressure, or both can lead to rodent biomass becoming elevated in degraded habitats (Lambert et al. 2006; Wells et al. 2007; Pimsai et al. 2014; Petersen et al. 2019). Leopard cats that specialise on rodent prey were also found to have a strong association with degraded landscapes with higher rodent populations (Petersen et al. 2019; Lambert et al. 2006; Rajaratnam et al. 2007; Wells et al. 2007; Pimsai et al. 2014). Support for the importance of artificial water on farmland comes from a study by Finerty and Macdonald (2019) who attributed a range expansion of servals to the exploitation of permanent artificial water sources on farmland. By contrast servals were absent in nearby wildlife management areas which typically have only seasonal water sources.

There are no other density estimates for serval in other protected reserves in South Africa limiting comparisons with other PAs and hence the generality of the suggestion that density will be lower within PAs compared to farmland. However, other studies on serval density within human modified landscapes suggest that serval may thrive in the absence of larger predators and with access to both abundant food supplies and permanent water. Thus, for example serval density in an industrial region of South Africa (Secunda Synfuels Operations plant) is the highest yet recorded (62.33 ± 2.1-11.55± 22.76 servals/100km^2) for this species throughout its range (Loock et al. 2018). The authors suggest that extraordinarily high density estimates may be attributed to the anthropogenically modified area providing protection from persecution by both larger carnivores and humans (Loock et al. 2018). Servals are the largest carnivore in the Secunda Synfuels Operations plant and thus have little interspecific competition from larger predators. In other areas, the presence of other medium- and large-bodied carnivores could otherwise limit serval population densities (through intraguild predation), so their absence can lead to mesopredator release, such as through increased survival of young (Ritchie and Johnson 2009). In addition, the disturbed habitat on the industrial site provides shelter and suitable food resources for rodents, and thus an abundant food source for servals allowing for a higher density (Taylor et al. 2013; Loock et al. 2018).

Longitudinal survey data (2013-2018) suggests that serval population densities in Ithala have decreased since the high of 9.66 (± 2.1) recorded in 2014 (see Figure 14. Leopard density estimates from the same time frame also show a decreasing trend, with a noticeable drop from 8.9 ± 1.7 leopards/100 km^2 in 2018 down to 3.8 ± 0.9 leopards/100 km^2 during the 2019 survey (see Figure 15). The northern border of Ithala is unfenced and is delimited by the Phongola River, which can be crossed at low points and during times of drought. Panthera cameras have previously been stolen in the northern section of the reserve with enough frequency that camera traps are no longer deployed in those areas. Manqele (2018) surveyed community members in the KwaZulu-Natal Midlands and found that most respondents of the survey anonymously admitted to hunting illegally to acquire meat and skins. Site-specific socio-economic drivers of illegal hunting for rural people living adjacent to PAs were unemployment and limited access to productive land and domestic sources of protein (Manqele et al. 2018). However, the primary driver of illegal wildlife hunting in the region was for sport by boys and young men, who were "bored" (Manqele et al. 2018). Snares and hunting dogs were cited as the primary methods of hunting. Snares, which were often set for other carnivores (i.g. black-backed jackal) are unselective and may snare servals as by-catch. Servals are readily bayed by dogs and are reported as being easy to hunt (Ray et al. 2005). Serval parts are used in muti and skins are commonly included as part of traditional or religious attire (Manqele et al. 2018).

Model Parameters

Servals are considered to be grassland and savannah wetland specialists (Geertsema 1985; Bowland and Perrins 1993; Thiel 2011; Ramesh and Downs 2015a; Edwards et al. 2018). Contrary to my predictions, vegetation type did not significantly impact the parameter estimates (D, σ and g*0*). This may reflect the low number of unique individuals and recaptures in the survey in addition to the limited variation in vegetation type amongst stations. Loock et al. (2018) identified that vegetation type had a significant effect on serval encounter rates. The authors reported that camera traps had highest capture rates in wetlands and lowest captures in grasslands. The null model was the strongest model based on AICc values and weights for all model parameters (see Table 11). When varying g*0* with the mean number of vehicles per day passing by each camera trap station, the model ranked a close second to the null model with a delta AICc of 2.89. This model was then compared to the null model using the likelihood ratio test and resulted in a p-value of 0.126 suggesting a weak effect of mean vehicles passing each camera station per day on the serval density estimates. Serval activity is lowest when vehicle activity is highest, but this is confounded by time of day with gate hours permitting vehicles to drive only between the hours of 05h00 to 19h00. Serval activity is reportedly strongly biased to crepuscular and nocturnal (Geertsema 1985; Thiel 2011; Ramesh et al. 2016a; Bohm and Hofer 2018) similar to the results obtained in this study (see Figure 12). Thus, the limited overlap of peak serval activity with peak vehicle activity may simply be an artefact of restricted vehicle times coinciding with preferred activity time for serval. When servals are active during the day then there was a slight trend for activity to drop during vehicle activity peaks (e.g. at 09h30 and 14h30) (Figure 12).

Conclusions, limitations and recommendations

The results presented here support the findings of Rocha et al. (2016) that camera trap surveys designed for larger carnivores can be used to estimate the density of smaller felids (Sollmann, 2014). Following the advice of Rocha et al., (2016) I reduced the mean intertrap distance within the leopard camera trap array to improve the precision of density estimates for a small felid. The smaller mean intertrap distance in addition to placement of camera traps within habitat assumed to be preferred by servals did increase the number of spatial recaptures as predicted by other studies (Efford 2012; Sun et al. 2014; Rocha et al. 2016) but there was limited improvement of the estimates of σ. Standard error for the leopard array and serval array were the same at 0.8 and the difference between the 95% upper confidence level and the 95% lower confidence level, also remained similar (and large) between the two arrays. While the density estimates did vary at 1.73 ± 0.77 (0.76-3.97) individuals/100 km² for the leopard array and 2.49 ± 0.81 (1.24-4.63) individuals/100 km² for the serval array, the confidence intervals suggest the two arrays produced overall very similar results.

Similar density estimates for both the serval and leopard specific arrays with overlapping confidence intervals suggested that long term data on serval from the Panthera leopard array may provide valid insights into serval density trends over time. While the standard deviation in the density estimate remained high across years there was a clear trend of declining serval density over the previous six years. Similar trends have been reported for leopard (Panthera, unpublished data, see Figure 15) with the lowest density estimates in 2019. Servals face many threats from habitat loss to direct persecution and illegal poaching (Thiel 2015; Ramesh et al.

2016a; Manqele et al. 2018). The northern border of the reserve is a river that is easily traversed on foot and many camera traps have been stolen from this section of the reserve. This suggests illegal activity in the area and a possible sink for wildlife targeted by poachers or captured as by-catch. Despite the growing availability of camera trap data, basic serval population data, and long-term population viability within protected reserves and agricultural landscapes remain understudied throughout their range. My study contributes to the current need for information on serval population density. To continue to fill this crucial knowledge gap, I recommend that more studies on servals within and outside of protected areas be conducted using small carnivore specific camera trapping arrays to improve density estimates. Additional comparison surveys with camera trap grids of various other large carnivores should also be conducted before a final protocol is implemented. I further recommend that camera trap surveys designed to quantify serval population densities make provision for recording higher resolution of vegetation unit classifications of the survey site. In addition to this, relevant biophysical and meteorological variables in the form of rainfall, altitude, and soil moisture should be recorded as relevant drivers of vegetation communities. When possible, camera traps utilising a rapid-fire camera function may lead to more accurate sexing of individual servals which may influence movement and density estimation. However, until funding for small carnivores improves, the results of this study suggest that using data from larger carnivore surveys can be an effective way of detecting long term trends in density estimates and provide an opportunity for wildlife managers to seek solutions to declining populations.

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