Population densities of mesocarnivores across protected and non-protected private landscapes in the Eastern Cape of South Africa

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Population densities of mesocarnivores across protected and non-protected private landscapes in the Eastern Cape of South Africa

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Population densities of mesocarnivores across protected and non-protected private landscapes in the Eastern Cape of South Africa

Abstract

Protected areas can be an effective tool for carnivore conservation, but increasing human populations are intensifying pressures and increasing negative interactions with wildlife. The conservation potential of private landscapes is being increasingly recognised to provide vital habitat and connectivity for wildlife. Due to their ecological and ethological plasticity, mesocarnivores thrive on a wide range of landscapes, but are frequently subject to intensive persecution outside of protected areas. Development of reliable and accurate monitoring methods is therefore vital to enable evidence-based decisions for achieving sustainable population management. Novel techniques have been developed to estimate population densities of unmarked species using camera trapping, but many of these methods require field validation. Using one such method, distance sampling with camera traps (CTDS), population densities of mesocarnivores were estimated across two adjacent properties in the Eastern Cape of South Africa: a mixed used agricultural area, and a 'Big Five' private game reserve. Evidence of a high density brown hyaena (*Parahyaena brunnea*) population was recorded within the protected site, whereas insufficient captures were obtained on the mixed-use agricultural area. Conversely, lower densities of black-backed jackal (*Canis mesomelas*) were found in the reserve than the agricultural landscape, indicating variable effects of land use on mesocarnivore density. However, high imprecision in density estimates was evident, primarily attributed to spatial heterogeneity in encounter rates. This study reinforces the importance of evaluating camera trap performance metrics for more accurate measures of sampling effort and suggests how a site-specific approach can increase the efficacy of CTDS for population monitoring when camera performance is extremely variable. Improving precision in estimates is vital to validate CTDS as a reliable monitoring practice, and future studies should aim to test ways in which survey design and sampling effort can affect confidence intervals, as well as evaluating performance against known population sizes or established density estimation techniques.

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Ethical approval was obtained from Durham University prior to the commencement of fieldwork.

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1. Introduction

1.1. Carnivore Conservation on Private Landscapes

Habitat loss driven by anthropogenic transformation represents a significant threat to biodiversity, with ecosystems increasingly at risk from habitat degradation and fragmentation (Pereira et al., 2010). Carnivore populations are particularly vulnerable to land use change (Schipper et al., 2008; Do Linh San et al., 2013; Júnior et al., 2022), and reduced area and quality of suitable habitat is driving range contractions and population declines (Di Minin et al., 2016; Wolf and Ripple, 2017). Globally, 54.3% of carnivore species' current range is comprised of high-quality habitat, of which only 5.2% is formally protected (Crooks et al., 2011). South Africa retains a diverse carnivore guild, but habitat loss, declines in prey abundances and persecution have resulted in widespread local extirpation of many species (*DEAT*, 2005).

Protected areas can be an effective tool for conservation (Brooks et al., 2006; Le Saout et al., 2013), providing 'refuges' for wildlife and often supporting higher overall biodiversity than adjacent non-protected landscapes (Wasiolka and Blaum, 2011; Lagesse and Thondhlana, 2016). However, the effectiveness of protected areas to conserve biodiversity in a rapidly changing world has been challenged (Rodrigues et al., 2004; Mora and Sale, 2011; Mascia et al., 2014). The current global protected area network is largely confined to areas unsuitable for human development (Joppa and Pfaff, 2010), and does not adequately reflect global biodiversity distributions (Brooks et al., 2004; Hoveka et al., 2020), or provide sufficient protection for terrestrial vertebrates (Rodrigues et al., 2004; Williams et al., 2022). Furthermore, the conservation potential of protected areas is increasingly undermined by the impacts of climate change (Hannah, 2008; Elsen et al., 2020), invasive species (Spear et al., 2013; Gallardo et al., 2017), landscape fragmentation (Newmark, 2008), and human encroachment around reserve boundaries (Woodroffe and Ginsberg, 1998; Bailey et al., 2016). In South Africa, formally protected areas make up 6% of land (*DSSA*, 2021), but increasing human populations and demand for space and resources is intensifying pressures and heightening negative interactions with wildlife (Bell et al., 2004; Di Minin et al., 2016; Willcox, 2020). Furthermore, as many species ranges extend beyond the coverage of the formal protected area network, private landscapes are being increasingly recognised for their conservation potential (Bond et al., 2004; Cousins et al., 2008; *DEA*, 2013; Clements et al., 2016, 2019; Pereira et al., 2020; Curveira-Santos et al., 2021a).

Private and working landscapes, including private conservation areas, commercial game breeding or hunting properties, and agricultural land make up 79% of land area within South Africa (*DRDLR*, 2013), and can provide valuable habitat and landscape connectivity for wildlife

(Kent and Hill, 2013; Ferreira et al., 2018). However, outside of formal protected areas, wildlife is often at heightened risk of anthropogenic mortality due to greater prevalence of pollution (Ramesh and Downs, 2015; Serieys et al., 2019), disease transmission from livestock or domestic animals (Hughes and Macdonald, 2013; Williams et al., 2019), road traffic collisions or intentional eradication regimes (Do Linh San et al., 2013). The diversity of land management approaches across South Africa are reflected in the highly variable levels of tolerance towards wildlife, leading to a patchwork of ecological coherence on private land across South Africa, with carnivore control often the primary focus of management regimes.

Lethal and non-lethal predator control methods are widely implemented on private landscapes to minimise economic losses. The extent of their implementation is generally dependant on the type and diversity of economic enterprises on the property, the tolerance of land managers, and even the landscape composition of the property (Thorn et al., 2013; Minnie et al. 2018a). Farms that raise small stock animals, or commercial game breeding properties with high densities of ungulates are more likely to implement lethal predator controls to reduce risk of stock depredation than properties that stock larger animals (Brink et al., 2021). On the other hand, commercial hunting properties may tolerate or even encourage predators if there is an economic benefit to their presence, such as trophy hunting or the control of other undesirable species (Lindsey et al., 2009; Treves, 2009; Crookes, 2023). Land managed for conservation tourism may promote or even reintroduce carnivores to attract wildlife viewing tourism or to preserve ecological processes (Linsey et al., 2009), but management of predators within small private reserves presents complexities, as populations must be monitored and managed to preserve ecological integrity, as well as optimising wildlife viewing experiences.

Private conservation areas, including nature and game reserves, generally aim to maintain diverse and abundant wildlife populations to attract tourism, but it is argued that many reserves may be too small to effectively conserve wide ranging species (Creel et al., 2013; Miller and Funston, 2014), and ecological integrity may be undermined by economic priorities (Lindsey et al., 2007; Maciejewski and Kerley, 2014; Clements et al., 2016). The prevalence of small (< 500 km^2), private game reserves is increasing across South Africa, and these areas now form a vital component of South Africa's area-based conservation targets (Bond et al., 2004; De Vos et al., 2019). In the Eastern Cape, many small private game reserves have been established by aggregating small farms into more economically viable conservation and ecotourism ventures (Langholz and Kerley, 2006; O'Brien, 2012). These reserves have restored severely overgrazed landscapes, and reintroduced extirpated wildlife to re-establish ecological processes and attract tourism (Hayward et al., 2007a; Newmark, 2008; Hayward and Kerley, 2009; Ferguson and Hanks, 2012). However, managing wildlife populations on relatively small, fenced reserves can present challenges, particularly for large predators that often require intensive management to avoid populations exceeding that which the reserve and available prey populations can support (Tambling and Du Toit, 2005; Hayward et al., 2007c; Kettles and Slotow, 2009; Miller and Funston, 2014; Clements et al., 2016). In the absence of effective management, rapidly expanding carnivore populations can decimate prey populations, as well as increasing the risk of mortalities from lethal encounters with conspecifics or other predators (Jiménez et al., 2019). Predator translocations from game reserves and conservancies are therefore commonly implemented to mimic natural migratory processes (Hayward et al. 2007a), but smaller bodied carnivores are rarely monitored as intensively. As small private reserves often share boundaries with working landscapes, carnivores breaching reserve borders can result in negative human-carnivore interactions within surrounding communities (Treves et al., 2003; Kesch et al., 2013; Banasiak et al., 2021a).

Outside of protected landscapes, large carnivores have been largely extirpated (Nowell and Jackson, 1996; Skead, 2007), and a resultant proliferation of some mesocarnivore species has occurred in the absence of their dominant competitors (Thorn et al., 2011; Taylor, 2015; Ramesh et al., 2017). Mesocarnivores, defined as any species occupying an intermediate trophic position in a food web, irrespective of size or taxonomy (Prugh et al., 2009), can thrive when larger predators are absent (Kamler et al., 2020c). Additionally, ecological plasticity of many species enable them to readily adapt and exploit novel resources on a range of anthropogenic landscapes (Kamler et al., 2012a; Ramesh et al., 2017; Minnie et al., 2018a). Land management practices outside of protected areas can also facilitate mesocarnivore population growth through increasing prey abundances (Byrom et al., 2014; Williams et al., 2019). As a result, rapidly expanding mesocarnivore populations can cause detrimental environmental and economic impacts on working landscapes (Prugh et al., 2009), with black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) most commonly implicated in livestock depredation, and consequently subjected to retaliatory or preventative persecution (Purvis et al., 2000; Woodroffe, 2000; Schuette et al., 2013; Pitman et al., 2017; Crookes, 2023).

South Africa has a highly diverse range of approaches towards wildlife management, and particularly mesocarnivore management. The mosaic of land-use types allows researchers to understand the complexities of ecological dynamics across a variety of systems, ranging from formal protected areas and private reserves with relatively intact wildlife assemblages, to hunting properties, commercial game ranches or livestock farms that often employ more invasive and intensive wildlife management. Resilience and adaptability of some mesocarnivore species can present significant challenges on both protected and non-protected landscapes, as individual and population level responses to management approaches are highly unpredictable and inconsistent across different land uses (Kamler et al., 2012a; Ramesh et al., 2017; Minnie et al., 2018a). Further research is needed into the population and spatial ecology of many species within this diverse group, as well as evaluation of the effectiveness of various predator management strategies. However, these goals are contingent on the development of accurate and reliable monitoring techniques (Kerley et al., 2017), which are vital to achieve sustainable population management while protecting livelihoods of coexisting communities (Van Eeden et al., 2018).

1.2. Factors Affecting Mesocarnivore Densities

Little is known about the spatial ecology of many mesocarnivore species across southern Africa (Easter et al., 2020; Wallin, 2022; Davis et al., 2023). Resource availability, interspecific interactions and anthropogenic disturbance are thought to be highly influential in determining carnivore densities on both protected and non-protected landscapes (Baker and Leberg, 2018), but the impacts are highly variable between species and environmental contexts (Sévêque et al., 2020). Understanding the complexities of environmental drivers of occurrence and the considerable interactions between these factors is essential for effective management and conservation.

1.2.1. Resource Availability

It is widely recognised that densities of carnivores are strongly related to available resources (Fuller and Kittredge, 1996; Carbone and Gittleman, 2002; Karanth et al., 2004). This is clearly demonstrated in black-backed jackal populations living near seal colonies in Namibia, where extremely high population densities and relaxation of territorial behaviour are observed in areas of abundant foraging resources (Hiscocks and Perrin, 1988; Nel et al., 2013). Similarly, higher densities of scavenging species are found in areas with greater carrion provisioning by large predators, and localised population abundance can increase in response to seasonal peaks in herbivore mortality (Forbes, 2011; Yarnell et al., 2013; Pereira et al., 2014; Fourie et al., 2015; Bashant et al., 2020). Outside of protected areas, abundance of livestock, ungulate calves (Klare et al., 2010; Drouilly et al., 2018), or small mammals (Byrom et al., 2014; Williams et al., 2019) can drive high densities of mesocarnivores on agricultural, livestock or game farming landscapes. Without sufficient prey available on anthropogenic landscapes, mesocarnivores are inhibited from colonising novel areas, despite reduced competitive pressures (Goodheart et al., 2021). For example, intensive livestock grazing can degrade vegetation, detrimentally impacting small mammal populations (Carbone and Gittleman, 2002; Blaum et al., 2007a) and adversely affecting their predators (Blaum et al., 2007b). On the other hand, intensive livestock grazing in some areas can facilitate optimal conditions for termite proliferation, which form an integral part of bat-eared fox (*Otocyon megalotis*) and aardwolf (*Proteles cristatus*) diets (Cooper and Skinner, 1979; Dalerum et al., 2016). Although density is strongly influenced by resource availability, the breadth and diversity of ecological niches occupied by mesocarnivore species results in inconsistent effects of changes to foraging resources community structure. Additionally, dietary plasticity of generalist mesocarnivores means they can easily adapt to changes in prey abundance (Minnie et al., 2018a), with cascading impacts on both intraguild community structure and biodiversity at lower trophic levels.

1.2.2. Interspecific Interactions

Interspecific interactions can significantly influence mesocarnivore densities, both through exploitation competition for space and resources, and interference competition by dominant predators (Creel and Creel, 1996; Creel, 2001; Caro and Stoner, 2003; Ritchie and Johnson, 2009; Swanson et al., 2014; Satgé et al., 2017). With the exception of leopard (*Panthera pardus*), apex predator populations in South Africa are largely confined to protected landscapes, where their presence significantly influences distribution, behaviour and community composition of the entire carnivora guild (Ritchie and Johnson, 2009; Newsome et al., 2017; Codron et al., 2018; Curveira-Santos et al., 2021b). Smaller bodied carnivores are vulnerable to mortality from direct lethal interactions with competitively superior predators (Prugh and Sivy, 2020; Curveira-Santos et al., 2022), as well as indirect impacts, such as kleptoparasitism, negatively affecting fitness (Caro and Stoner, 2003), although variable impacts are observed between species (Begg et al., 2013; Allen et al., 2018). As a result, mesocarnivore distributions within protected areas often reflect spatial avoidance of dominant carnivores by subordinate species, with mesocarnivores more heavily utilising areas of high anthropogenic disturbance that are generally avoided by larger carnivores (Balme et al., 2010; Taylor, 2015; Newsome et al., 2017; Tambling et al., 2018; Curveira-Santos et al., 2021b). As a result of these competitive pressures, mesocarnivores can occur at lower population densities within protected areas than comparable areas where large predators are absent (Prugh et al., 2009; Taylor, 2015; Pretorius, 2019; Hardouin et al., 2021).

In the absence of suppression by apex predators, rapid population growth and range expansion in subordinate predator populations may occur, a process known as 'meso-predator release' (Prugh et al., 2009). This has been observed in the rapid expansion of black-backed jackal and caracal populations in South Africa following local extirpation of apex predators across agricultural land (Kamler et al., 2012a; Taylor, 2015; Ramesh et al., 2017; Drouilly et al., 2018; Van der Weyde et al., 2018). In addition to significant economic damage through livestock depredation (Thorn et al., 2015), high densities of mesocarnivores can have wide ranging ecological impacts, through suppression of subordinate carnivores (Prugh et al., 2009; Ritchie and Johnson, 2009; Kamler et al., 2012b). For example, Cape fox (*Vulpes chama*) found to be significantly less abundant in the Northern Cape on properties where black-backed jackal were present compared to properties where they had been eradicated, despite similar habitat characteristics and resources (Kamler et al., 2013). Direct resource competition between caracal and black-backed jackal also heavily influences population densities (Melville, 2004; Klare et al., 2010; Loveridge and Nel, 2013; Kamler et al., 2020c), with high caracal densities found in areas of low jackal density, and vice versa (Pohl, 2015). As a result of these highly complex interspecific interactions, it becomes difficult to derive conclusions about the degree of influence different factors present to mesocarnivore densities across different land uses, with wide reaching implications for species conservation management.

1.2.3. Anthropogenic Disturbance

Anthropogenic disturbance unquestionably influences density of mesocarnivore populations, with impacts most acutely observed outside of protected reserves on human-dominated landscapes (Purvis et al., 2000; Woodroffe, 2000; Crooks, 2002; Schuette et al., 2013; Curveira-Santos et al., 2021a). High mortality resulting from human activities, presence of domestic animals and livestock (Hughes and Macdonald, 2013; Williams et al., 2019), pesticide use (Ramesh and Downs, 2015; Serieys et al., 2019) and hunting practices (Do Linh San et al., 2013) can cause high mortality outside of protected areas, resulting in complex source-sinks dynamics across heterogenous landscapes (Minnie et al., 2018b). Despite decades of persecution and lethal population management strategies, livestock depredation continues to cause significant economic disruption to the agricultural economy of South Africa (Avenant and Du Plessis, 2008; Minnie et al., 2018a), and mesocarnivore eradication regimes are commonly implemented to reduce, or in response to, livestock depredation (Purvis et al., 2000; Inskip and Zimmerman, 2009; Schuette et al., 2013; Crookes, 2023). In some areas, hunting can replicate natural mortality levels of black-backed jackal populations exposed to lethal interactions with apex predators (Treves and Naughton-Treves, 2005; Haswell et al., 2017; Kamler et al., 2020b), potentially neutralising any detrimental impacts from meso-predator release (Blaum et al., 2010). Continuous, high intensity hunting can maintain very low population densities or even eradicate targeted mesocarnivores (Kamler et al., 2013), but involve significant time and resources to maintain over time. On the other hand, lethal control measures in some areas may inadvertently inflate black-backed jackal abundance due to compensatory reproductive mechanisms and immigration into vacant territories (Nattrass and Conradie, 2013; Wielgus and Peebles, 2014; Minnie et al., 2016). For example, reducing population size increases resources available for surviving individuals, allowing previously subordinate individuals to reproduce earlier and more successfully (Minnie et al., 2016). The complexity of responses present a significant challenge when considering predator management approaches, and the extent to which measures impact mesocarnivore communities is largely unknown, particularly in regard to the potentially cascading effects on ecosystem functioning.

The impacts of predator management strategies on working landscapes can severely impact populations and ecosystem function, but effects are highly context dependant, with considerable variation observed between land uses and individual species responses (Ritchie and Johnson, 2009; Kamler et al., 2013; Haswell et al., 2017; Curveira-Santos et al., 2019; Gigliotti et al., 2020; Pardo et al., 2022). Non-selective predator control measures can adversely impact non-target species, with honey badger (*Mellivora capensis*), aardwolf, and bat-eared fox particularly susceptible to non-selective predator control measures (Do Linh San et al., 2013, 2016; Treves et al., 2016; Pretorius, 2019). In the Kalahari, predator control measures negatively affected black-backed jackal, African wildcat (*Felis lybica)*, and caracal, whereas bat-eared fox, cape fox, and small-spotted genet (*Genetta genetta*) were positively affected (Blaum et al., 2010). Positive responses of some species to lethal management are presumably due to reduced competitive pressure from more dominant intraguild species, highlighting the complexity of intraguild responses to anthropogenic management.

Although the impacts of anthropogenic disturbance are most acute on human-dominated landscapes, protected reserves are not immune from the effects of human activity, and management policies can influence the density and distribution of mesocarnivores within reserves. Some protected areas actively cull mesocarnivore populations to reduce predation pressures on ungulate populations (Nattrass and Conradie, 2015; Minnie et al., 2016), and management of vegetation structure through herbivory exclusion zones or fire regimes can affect community structure (Roemer et al., 2009; Clavel et al., 2011). Additionally, permeability of fence lines can influence densities by facilitation or prevention of dispersal processes (Edwards et al., 2020; Williams et al., 2021a), as well as impacting the level of encroaching anthropogenic disturbances along reserve edges (Woodroffe and Ginsberg, 1998; Balme et al., 2010).

Anthropogenic activities are increasingly impacting populations of mesocarnivores, both within and outside of protected landscapes. While generally considered detrimental, the impacts of anthropogenic activities on wildlife densities are highly dependent on the intensity of disturbance, the species affected, and the environmental context. Comprehension of the interactive processes that drive mesocarnivore density is invaluable for species conservation and sustainable population management, but gaining this understanding relies upon accurate and reliable data for a highly diverse, and difficult to monitor, taxa.

1.3. Density Estimation Methods

Monitoring trends in wildlife populations is the cornerstone of effective management and conservation (Stem et al., 2005). Measures of population density can provide insight into both abundance and distribution of wildlife, allowing for direct comparisons between different populations of the same species. However, accurate measures of population size and abundance can be difficult to obtain, particularly for highly elusive species and for populations that occur over large areas (Kery et al., 2010; Bischof et al., 2014; Satterfield et al., 2017).

Advances in remote camera trapping technology have allowed researchers to monitor elusive species with minimal disturbance (Rowcliffe and Carbone, 2008; Rovero and Zimmermann, 2016; Agha et al., 2018), and novel methods to derive meaningful abundance estimates from camera trap data are constantly in development. Capture-mark-recapture (CMR) methods using camera trapping have been widely applied to large carnivores (Chase Grey et al., 2013; Swanepoel et al., 2015; Fouché et al., 2020), as well as some smaller felids with uniquely distinguishable markings (Anile et al., 2012; Caruso et al., 2012; Thornton and Pekins, 2015). However, methods requiring identification of individuals in a population cannot be applied to many mesocarnivore species that do not have distinct pelage patterns. Without the ability to recognise individuals, population density estimates have relied on indirect measures, such as photographic detection rates, which are generally not considered reliable abundance predictors, being overly simplistic and failing to account for variable detection probabilities (Carbone et al., 2001; Jennelle et al., 2002; Rovero, and Marshall, 2009; Sollmann et al., 2013; Burton et al., 2015). Consequently, alternative methods have emerged to calculate density without the need for individual recognition, including the Random Encounter Model (REM; Rowcliffe et al., 2008), the Random Encounter Staying Model (REST; Nakashima et al., 2018), and distance sampling using camera traps (CTDS; Howe et al., 2017).

Eliminating the need for individual recognition in density estimation can increase the applicability of camera trapping for estimating densities of unmarked species and offer multiple advantages over CMR methods. REM, REST and CTDS all allow for more flexibility in sampling designs and can target multiple species during one survey period (Cappelle et al., 2021; Palencia et al., 2021a). Furthermore, these methods eliminate the need for assumptions around spatial autocorrelation in captures, as required by mark-recapture methods, reducing the minimum number of captures required for analysis (Palencia et al., 2021a). These methods have the potential to provide robust density estimates of unmarked species, but each have specific caveats and ways of addressing violation of assumptions that affect suitability which must be carefully considered before their application (Cappelle et al., 2021; Gilbert et al., 2021; Palencia et al., 2021a; Morin et al., 2022).

The Random Encounter Model (REM) is derived from the ideal gas theory, wherein animal movement is likened to the random movement of gas particles (Hutchinson and Waser, 2007). Density is estimated by accounting for the relationship between encounter rate, the effective field of view of the camera trap, and the speed of animal movement (Rowcliffe et al., 2008). Since being proposed, REM has been widely developed (Lucas et al., 2015; Jourdain et al., 2020), and tested on a range of species (Zero et al., 2013; Pfeffer et al., 2018; Kavčić et al., 2021), including carnivore populations (Manzo et al., 2012; Anile et al., 2014; Cusack et al., 2015a). When compared to capture-recapture or other unmarked density models, this method appears to produce comparable estimates, although some studies have reported higher estimates using REM than alternative techniques (Anile et al., 2014; Palencia et al., 2021a; Pettigrew et al., 2021; Santini et al., 2022; Twining et al., 2022). Like most modelling approaches, REM relies on accurate data for model parameters, which can be difficult to measure. Estimates of animal speed of movement are particularly difficult to reliably obtain at a sufficient temporal resolution (Rowcliffe et al., 2012), and can significantly influence estimates and precision (Melville and Strauss 2021; Santini et al., 2022). Previous application of REM have relied upon data from GPS collars or from following habituated populations to estimate animal speed of movement (Cusack et al., 2015a; Caravaggi et al., 2016; Pettigrew et al., 2021), but more recent developments have allowed estimation directly from camera trapping data, significantly increasing the applicability of the method (Rowcliffe et al., 2016; Palencia et al., 2021b).

The Random Encounter Staying Time model (REST) builds upon the REM by discarding the need for animal movement data, instead describing the relationship among staying time, trapping rate, and density (Nakashima et al., 2018). By incorporating staying time of animals in front of the camera as an alternative to speed of movement, REST offers a less expensive and time-saving alternative to REM when animal movement data is not available, as staying time can be estimated relatively quickly from videos or consecutive photo bursts (Palencia et al., 2021a; Santini et al., 2022). An advantage of REST over REM is the ability to incorporate environmental covariates into density estimates, allowing spatial variation in denisty to be modelled across heterogenous environments (Nakashima et al., 2018). To date, the REST model has been applied to estimate the density of forest ungulates (Nakashima et al., 2020) and tested with human volunteers (Garland et al., 2020).

CTDS is adapted from well-established distance sampling theoretical framework which forms a cornerstone of wildlife monitoring (Buckland et al., 2001; Thomas et al., 2010; Howe et al., 2017). Conventional distance sampling uses point or line transect surveys to detect animals at recorded distances from the observer, which are then fitted to a detection function to estimate detection probability at increasing distance from the observer, while accounting for imperfect detection (Buckland et al., 2001; Borchers et al., 2002; Thomas et al., 2010). Using human observers to conduct wildlife surveys can be costly and time consuming, and human presence may impact detectability of some species (Buckland et al., 2001). This issue may be particularly challenging outside of protected areas where human activity and wildlife persecution is more prevalent, and populations are therefore more alert to human presence (Suraci et al., 2019). By adapting traditional point transect distance sampling methods for use with camera traps, CTDS allows for continuous, non-invasive sampling, reducing the potential for low detection due to human disturbance, and increasing the applicability of camera trapping to monitor rare or elusive populations (Palencia et al., 2021a).

Field tests of CTDS have been conducted on populations of chimpanzees (Cappelle et al., 2019), marmots (Corlatti et al., 2020) and mountain ungulates (Harris et al., 2020; Pal et al., 2021), and comparable estimates have been produced by CTDS in relation to known population sizes and alternative density estimation methods (Howe et al., 2017; Harris et al., 2020; Cappelle et al., 2021). Previous studies have also built upon original methodology to increase the applicability of CTDS for monitoring rare or fast-moving species, as well as allowing flexibility in camera trap settings (Corlatti et al., 2020; Mason et al., 2022; McKaughan et al., 2023). However, estimates for exceptionally rare species may be too imprecise (Cappelle et al., 2021), and bias in density estimates may occur for species that show high reactivity to camera traps (Houa et al., 2022; McKaughan et al., 2023).

Identifying one optimal method to estimate densities of unmarked populations is a significant challenge, as each method has been found to be more applicable under different scenarios (Gilbert et al., 2021; Palencia et al., 2021a). Palencia et al. (2021a) evaluated the performance of REM, REST and CTDS, applying each to the same mammalian populations. Although the three methods did not predict significantly different density values in most populations tested, Palencia et al., (2021a) concluded that REST is most suitable for high abundance species, whereas REM is recommended when camera trap performance is suboptimal, and preferred over REST when fewer camera traps are available (Palencia et al., 2021a; Santini et al., 2022). CTDS is reportedly more suited to low abundance populations, as multiple data points can be obtained from one capture occasion, increasing potential sample size from relatively few independent encounters (Palencia et al., 2021). For this reason, CTDS has emerged as a promising method to monitor mesocarnivore communities that often occur in low abundances and has previously been applied to populations in the Democratic Republic of the Congo (Bessone et al., 2020), the UK (Mason et al., 2022), and South Africa (McKaughan et al., 2023).

Numerous developments have been proposed to the original CTDS methodology to increase its effectiveness under different scenarios. Mason et al. (2022) successfully applied CTDS to populations of two mesocarnivores, European badger (*Meles meles*) and red fox (*Vulpes vulpes*) while investigating the performance of CTDS when applied to both survey-wide and habitat-specific areas. Reported densities were within the range of previously published estimates, and despite large confidence intervals, were amongst the most precise produced for the species at the time of publication. Similarly, CTDS produced estimates largely within the expected range for four mesocarnivore species in the Limpopo region of South Africa, although variance was high (McKaughan et al., 2023). Additionally, McKaughan et al. (2023) evaluated the methodological elements of CTDS regarding both survey design and calculations of survey effort, revealing significant variation in estimates according to the analytical method applied (See section 2.4.2). Continual testing of the method is still required to assess the robustness under different study designs and ways to improve precision, the development of which is vital to derive meaningful conclusions from estimates that can be incorporated into conservation and management planning.

1.4. Rationale and Research Questions

Population monitoring is an essential part of wildlife management on both protected and non-protected landscapes, and is vital to inform decisions around reintroductions, population management, or sustainable harvesting quotas. Mammalian predators are widely studied across South Africa, but there is disparity in research efforts, with greater focus on larger species, and populations within protected areas (Agha et al., 2018; Balme et al., 2014; Brooke et al., 2014; Fazey et al., 2005; Small, 2011). Smaller bodied carnivores are comparatively understudied (Brooke et al., 2014), and population trends for half of all species in mainland Africa are unknown (Do Linh San et al., 2013). This research deficiency has led to a lack of robust data, which is vital to reliably inform extinction risk (Do Linh San et al., 2013; IUCN, 2022).

The ecological role of smaller bodied carnivores is becoming increasingly recognised (Roemer et al., 2009; Williams et al., 2019), with evidence of some species facilitating nutrient cycling (Schmitz et al., 2010; Gharajehdaghipour et al., 2016; Kucheravy et al., 2021), seed dispersal (Herrera, 1989; Hamalainen et al., 2017; Kamler et al., 2020a; Rubalcava-Castillo et al., 2021; Nakashima and Do Linh San, 2022), and organic waste disposal by scavenging from larger predator kills or livestock carcasses (Ćirović et al., 2016; Prugh and Sivy, 2020). Predation on agroecosystems can provide biological control of rodent populations, reducing crop losses (Williams et al., 2019) and transmission risk of zoonotic diseases (Ostfeld and Holt, 2004; Levi et al., 2012). Marneweck et al. (2022) recently highlighted the role of small carnivores as sentinels of global change, wherein behavioural or population level changes can indicate wider ecological shifts and changes in ecosystem function. However, detecting these changes requires reliable population monitoring, and the highly elusive nature of smaller bodied carnivores presents challenges for capturing the quantity and quality of data required to reliably estimate population size or density (Brooke et al., 2014). Development of techniques to monitor abundances of populations is therefore vital for understanding the natural and anthropogenic factors that influence mesocarnivore populations, as well as to identify and mitigate threats to at-risk populations.

This study aims to assess the efficacy of CTDS in determining mesocarnivore densities within a private game reserve and an adjacent mixed-used agricultural area in the Eastern Cape of South Africa. Densities of target species will be estimated across both landscapes, providing vital data for both reserve and agricultural management, as well as contributing to wider ecological understanding of understudied carnivora species.

Key Aims and Objectives

- To investigate the ability of CTDS to estimate densities of mesocarnivores under different analytical approaches.
- To estimate density of mesocarnivore populations within a protected, private game reserve and an adjacent mixed use agricultural area.
- To compare population densities of mesocarnivores across different land uses.

2. Methods

2.1. Note on fieldwork

Fieldwork was initially planned to take place within Umfurudzi Park, Zimbabwe through a collaborative project with Zimbabwe National Parks and a newly established conservation and sustainable development initiative. This project intended to use camera traps to estimate densities of mesocarnivores within the park, as well as providing baseline data for all wildlife populations to inform potential reintroductions and future monitoring. The acquisition of research permits presented an initial delay to the commencement of fieldwork until May 2022. After receipt of necessary permits, I travelled to South Africa prior to commencement of planned fieldwork to source and test equipment before intending to travel to Zimbabwe.

Unfortunately, logistical challenges with the establishment of the wider project at Umfurudzi Park resulted in the last-minute cancellation of the project, making it impossible to conduct fieldwork as planned. As a result, it became necessary to reconfigure the project on a new field site in the Eastern Cape of South Africa using limited time and resources available. Through a collaboration with the management team at Shamwari Private Game Reserve and the landowner of an adjacent property, I was able to amend the aims of the initial study to investigate comparative densities across two contrasting landscapes, while retaining the core methodological approaches of the original project.

2.2. Study Area

The study area falls within the Alexandria and Albany districts of the Eastern Cape, approximately 85 km north-east of Gqeberha (33°21'29.7"S 26°11'57.3"E; Figure 1), and on the western edge of the Maputaland-Pondoland-Albany Global Biodiversity Hotspot, recognised for its high biodiversity and endemism (*CEPF*, 2010). A camera trapping survey was conducted across two adjacent properties: a mixed used agricultural area (MUA), and Shamwari Private Game Reserve (SGR). Established in 1990, SGR is a protected, 180 km² private game reserve managed primarily as a five-star ecotourism destination. Since its establishment in 1990, SGR has consolidated and restored farmland for the aim of conserving floral and faunal biodiversity (Joubert and O'Brien, 2005; "The Shamwari Story," 2023).

A camera trapping survey was conducted across an approximately 21 km^2 subsection of SGR, in an area appended to the existing reserve in 2007 and most frequently used by the reserve's conservation volunteer experience. The MUA is approximately 11.5 km^2, with a northern and southern section separated by a public road, and internal cattle fencing throughout. The property is bordered by electrified game fences on all sides, and is primarily used for grazing and breeding cattle, as well as olive plantations (approximately 0.3 km^2), and infrequent game hunting. Anthropogenic activities on the MUA are more concentrated on the south side of the public road, whereas sections of the northern side of the property are rarely visited by humans or livestock. Both study sites contain permanent water sources, residencies, and commercial properties, and are separated by an electrified "predator-proof" game fence.

2.2.1. Historical and Current land use

This region was largely considered unsuitable for intensive agriculture by European settlers, and cultivation was generally restricted to alluvial soils near permanent water (Lubke et al.1986. Livestock grazing has been, and continues to be, the primary production of the region (Lubke et al.1986; O'Brien, 2012). However, intensive overgrazing, high labour costs, and prolonged periods of drought have resulted in a shift from pastoralism towards more economically viable game farming or tourism ventures since the 1980s (Smith and Wilson 2002; Sims-Castely et al., 2005; Langholz and Kerley 2006; Cousins et al., 2008; Hamann and Tuinder, 2012). Through acquisition and aggregation of multiple small farms, numerous small (< 500 km^2) private game reserves have been established in the region (Langholz and Kerley, 2006). These reserves have restored overgrazed landscapes and reintroduced wildlife for the purpose of offering wildlife viewing experiences in a malaria-free area (Castley et al., 2001; Hayward et al., 2007a). SGR was one such reserve, established in 1990 with the acquisition of farmland that had been rendered economically inviable by prolonged period of droughts (O'Brien, 2012).

2.2.2. Climate

Falling between the Mediterranean climate in the Western Cape and the subtropical climate in Kwa-Zulu Natal, the Eastern Cape experiences a highly varied climate. Rainfall patterns are bimodal, with a summer rainfall zone in the east and a winter rainfall zone in the west (Hamann and Tuinder, 2012). The study area falls within the winter rainfall zone, receiving a mean annual precipitation of 598mm, peaking in the spring (Hijmans et al., 2005; Mahlalela et al., 2020). With an altitudinal range of 380 – 689m, the mean minimum temperature is 8°C in the winter, and mean maximum temperature is 30°C in the summer months (Zhang et al., 2019), with landowners reporting maximum temperatures of up to 47°C (per comms with local landowners).

The Eastern Cape of South Africa has suffered a severe drought since 2015, and the province was declared a 'drought disaster region' in 2019 due to severe water shortages in many rural and urban areas (Mahlalela et al., 2020). As a result, many previously permanent water sources within the MUA dried up in 2019, and SGR have provided artificial watering points throughout the reserve (per comms with reserve management).

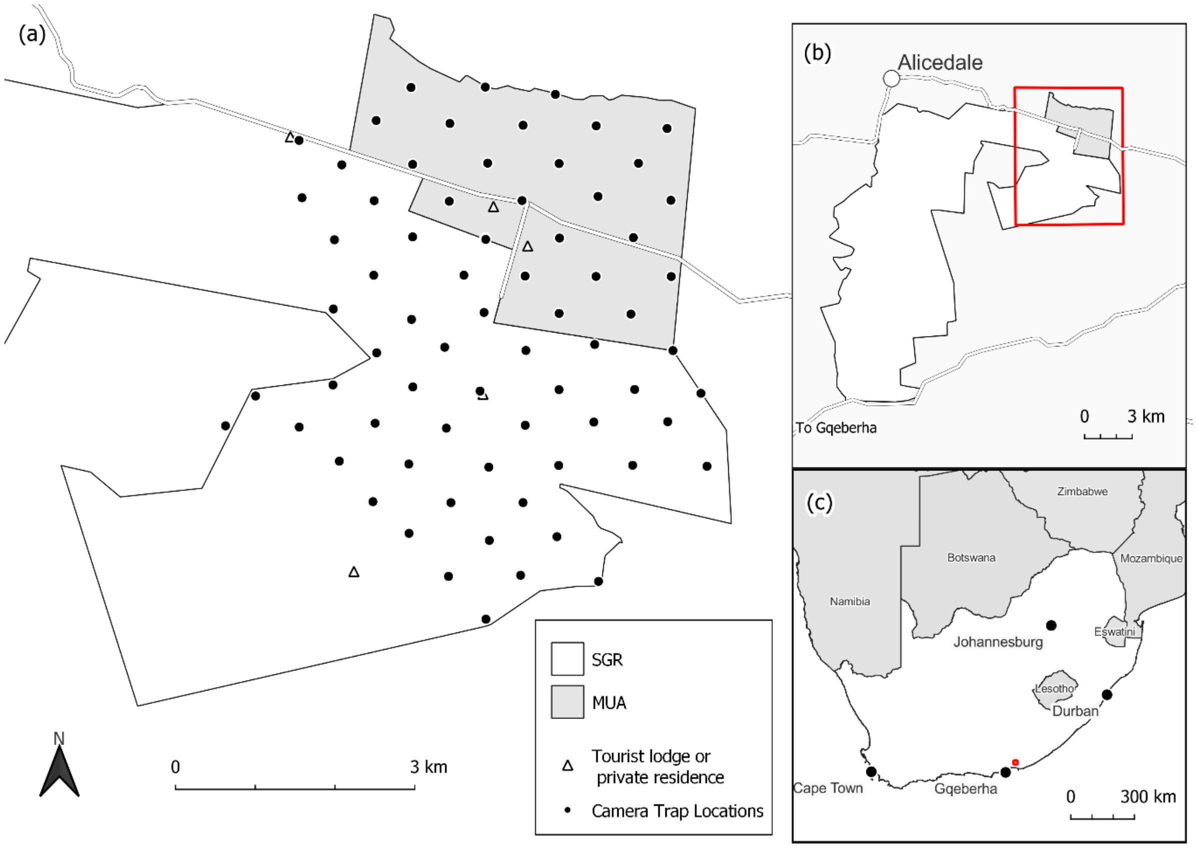

Figure 1. Study area was located on two adjacent properties in the Eastern Cape province of South Africa; (a) a mixed-use agricultural area (MUA) and a protected area; Shamwari Private Game Reserve (SGR); (b) The subsection of SGR where camera trapping took place; (c) National context of the study area.

2.2.3. Vegetation

Hosting all of South Africa’s biomes, the Eastern Cape is recognised for varied and diverse floral communities that developed as a result of the climatic, geomorphological, and geological conditions of the area (Lubke et al., 1986). Variable rainfall patterns across the province results are reflected in variable growing seasons, with the central and western regions predominated by C3 grasses that favour caprinae livestock production (Hamann and Tuinder, 2012).

Five recognised South African biomes are found within SGR: savanna, thicket, grassland, forest and fynbos, three which occur within the camera trapping survey area (fynbos, savanna, and thicket biomes). Within these biomes, with five distinct units are found, which represent vegetation community groups sharing similar biotic and abiotic features (Figure 2; Mucina and Rutherford, 2011). Within the thicket biome, SGR contains large areas of Grahamstown Grassland Thicket, characterised by a mosaic of low thicket patches and grassland, in addition to small areas of Albany Valley Thicket consisting of medium to tall thicket vegetation, dominated by small trees and woody shrubs (Hoare et al., 2006). The only unit of savanna biome in the study area is Bhisho thornveld, occurring primarily on undulating and moderately steep slopes or drainage valleys across both SGR and the MUA. This unit is characterised by open savanna; small trees with short-medium dense grassland understorey (Rutherford et al., 2006). Two fynbos units are found within both study sites; large areas of Suurberg Quartzile Fynbos, and smaller patches of Suurberg Shale Fynbos. Both fynbos units occur on low rounded hills and mountains, and support low-medium high ericoid shrubland or grasslands, with understorey comprised of restioid or grasses (Rebelo et al., 2006). The distinction between quartzite and shale fynbos is thought to primarily concern the geology of their habitats, but further research is needed to confirm physically distinct characteristics between these two units (Rebelo et al., 2006).

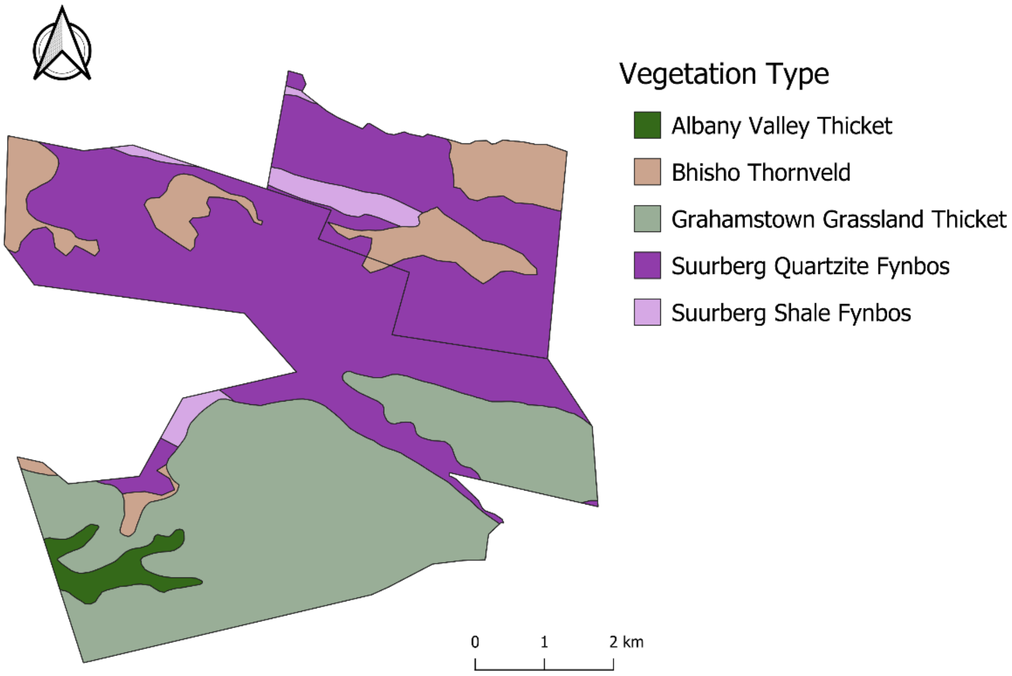

Figure 2. Natural vegetation units found within the study area according to the vegetation classification system of South African National Biodiversity Institute (Mucina and Rutherford, 2011; SANBI, 2018).

Having previously been used for intensive caprinae livestock farming, both sites also show evidence of severe overgrazing, with some areas considered ‘disturbed lands’ as they no longer conform to any natural vegetation (O’Brien, 2012). Additionally, vegetation structures of the same vegetation unit are likely to demonstrate physical variation due to the foraging behaviour of elephants (*Loxodonta africana*) on SGR (Cowling and Kerley, 2002).

2.2.4. Wildlife

After the arrival of 1820s European settlers and subsequent onset of intensive agriculture, the majority of large predators were eradicated from the Eastern Cape (Skead 2007). Leopard are thought to have persisted in the region at low densities, primarily in remote areas away from human settlement (Skead, 2007, Minnie et al., 2015). Although both brown and spotted hyaena (*Crocuta crocuta*) were historically recorded in the Eastern Cape, very few instances of brown hyaena were recorded in the region, and the species was considered extirpated in the 1980s (Skead, 2007; Stuart, 1981).

As part of ecological restoration, as well as to attract tourism, native wildlife has been reintroduced into SGR, in addition to extra-limital species such as white rhinoceros (*Cerathotherium simum*) and giraffe (*Giraffa giraffa*; Castley et al., 2001; Maciejewski and Kerley, 2014). The first herbivores were reintroduced into the reserve in 1992, with predators following in 2000, marking the first reintroduction of free roaming large carnivores into the Eastern Cape (O'Brien, 2012). Reintroduced carnivores included lion (*Panthera leo*), wild dogs (*Lycaon pictus*), brown hyena (*Parahyaena brunnea*), cheetah (*Acinonyx jubatus*) and serval (*Leptailurus serval*), as well as additional leopard (Hayward et al., 2007a; O'Brien, 2012). With the exception of wild dogs that were removed from the reserve due to repeated escapes and pressure on prey stocks, these reintroductions have been considered largely successful (Hayward et al., 2007b; Banasiak et al., 2021b). SGR now contains the 'Big Five'; lion, leopard, elephant, rhinoceros (*Cerathotherium simum* and *Diceros bicornis)* and African buffalo (*Syncerus caffer*). Aside from brown hyaena and serval, mesocarnivores have not been actively reintroduced in the reserve, and species present today are believed to have persisted in the area or recolonised naturally, including black-backed jackal, caracal, honey badger, aardwolf and bat-eared fox (Hayward et al., 2007a; O'Brien, 2012).

In terms of mammalian herbivore populations, both SGR and the MUA support populations of greater kudu (*Tragelaphus strepsiceros*), mountain reedbuck (*Redunca fulvorufula*) and waterbuck (*Kobus ellipsiprymnus*), as well as smaller ungulates such as common duiker (*Sylvicapra grimmia*) and bushbuck (*Tragelaphus sylvaticus*). Aside from a breeding herd of blesbok (*Damaliscus pygargus phillipsi*), the MUA has not intentionally stocked ungulate species on the property, whereas SGR supports numerous populations, including zebra (*Equus quagga burchellii*), black wildebeest (*Connochaetes gnou*), red hartebeest (*Alcelaphus buselaphus caama*), sable (*Hippotragus niger*), impala (*Aepyceros melampus*) and springbok (*Antidorcas marsupialis*).

Private game reserves such as SGR are legally required to install electrified "predator-proof" game fencing to separate wildlife from adjacent farmlands and communities, which aims to protect “managed wild populations”, prevent disease transmission to livestock and avoid human-wildlife conflict (Hayward and Kerley 2009). However, despite fencing, increasing occurrences of negative human-wildlife interactions have been reported in this region of the Eastern Cape since the establishment of private game reserves (Banasiak et al., 2021a), with the local farming community reporting a perceived increased livestock depredation by primarily caracal and black-backed jackal (Van Niekerk, 2010; Banasiak et al., 2021a). As a result, mesocarnivores are widely considered ‘pests’, and professional culls, opportunistic shooting, and hunts using dogs are conducted in the area. Although hunting of black-backed jackal has occurred on MUA in the past, no carnivores were hunted or culled on the MUA during the study period.

2.3. Fieldwork

Sixteen camera traps (Bushnell Single Core 119938C; Browning Recon Force Extreme BTC-7FHD-PX) were rotated over 71 sites to survey for mesocarnivores in SGR and the MUA between August and November 2022. Camera locations were predetermined using QGIS (version 3.2.0, 2022) and placed at the intersections and central points of a systematic 1 km x 1 km grid with a random origin (Figure 1). A systematic, random sampling design was applied to adhere to the assumption that points are independent of animal location, reducing potential bias in estimates that would occur if cameras were placed on roads or trails that are preferentially used by many species (Howe et al. 2017; See Section 4.2.2). By spacing camera traps in relation to the home ranges of target species, the risk of double-counting individuals can be reduced. However, when undertaking multi-species surveys, cameras must be spaced appropriately to reflect variable home ranges of all members of the target guild and ensure all individuals within the study area have an equal chance of being detected. Considering this, cameras were placed within a finer scale grid than would be expected to solely capture larger-ranging species such as brown hyaena, than species such as mongooses (*Herpestidae sp.*) or genets (*Genetta sp.*).

Cameras were deployed as close as possible to the pre-determined point and oriented south (± 30°) to avoid overexposure to sunlight. Where sites were impossible to access or there were no suitable mounting points, cameras were placed in the nearest suitable location, without intentionally targeting areas that would increase detection probability. The absence of trees in the thicket vegetation biome posed a challenge in identifying appropriate and stable natural mounting points near the designated location for camera placement. The use of artificial mounting posts was considered, but this was not encouraged by land managers in the study area due to high likelihood of elephant and livestock interference. Consequently, deviations from the designated points were frequent (mean 44.0 m; range 2.7 - 220.7 m), and the mean camera spacing of deployed cameras was 720.17 m (range 579.8 - 856.1 m).Camera height varied between 40-100 cm to allow for more stable installation, and cameras were angled approximately level to the ground. Vegetation directly obscuring the field of view was cleared to avoid repeated false triggers, but efforts were taken to ensure vegetation removal was minimal to preserve important floral diversity of SGR.

Cameras were active for 24 hours a day and programmed to capture between three and five images of 8MP resolution when triggered, with a five to ten second trigger interval between potential successive capture events. Specific settings at each site were determined based on vegetation characteristics and the likelihood of false triggers. For example, where cameras were deployed at sites where vegetation movement was likely to trigger the camera frequently, the number of images in a burst was reduced, and the interval between potential triggers was extended to conserve battery life for the duration of the sampling period. Each camera was active for approximately fourteen days (mean 14.4 days; range 12 – 23 days), before being relocated to a new survey site, at which time batteries were replaced where necessary, and memory cards were downloaded. A migrating camera trap grid was chosen to increase the number of sampling locations and maximise coverage of the study area given the limited number of camera traps available. Considering CTDS can include multiple data points from non-independent capture occasions (see Section 2.4.1. Camera Trap Distance Sampling), the potential double counting of individuals was not considered to influence results (Cappelle et al., 2021, McKaughan et al., 2023). In the event of battery failure or cameras being moved or damaged within 10 days of deployment, cameras were redeployed for an additional survey period. One pre-determined point located directly on the fence separating the two study sites was sampled on both properties.

Videos of researchers walking across the field of view highlighting distances at 3, 5, 8, 10, 12 and 15m from the camera were taken on collection of each camera trap (Howe et al., 2017; Figure 3). These videos served as a reference for estimating radial distances from the camera lens to the midpoint of target species captured.

Figure 3. Screenshot from reference videos taken on collect of each camera trap, used to estimate radial distances from the camera to the midpoint of the detected animal. Image shows researcher walking across the camera field of view with a tape measure indicating 5m distance.

All images were examined manually using photo management software 'digikam' (version 6.2.0; www.digikam.org), with mammalian captures identified and assigned a metadata species tag. Distances for each capture of target species were tagged in increments of 0.5-meter intervals up to 8m, 1-meter intervals from 8m to 15m, and distances beyond 15m were allocated '15+'. Tags and metadata were extracted and subsequently managed in R using camtrapR version 2.2.0 (Niedballa et al., 2016; R Core Team, 2022).

2.4. Data Analysis

2.4.1. Camera Trap Distance Sampling

In CTDS, density ($\hat{D}$) is estimated as:

$$\hat{D} = \frac{n_k}{\pi w^2 e_k \hat{P}_k}$$

where n_k is the number of observations of animals at a given sampling location (k), w is the truncation distance beyond which any recorded distances are discarded, e_k is the sampling effort expended at point *k* (See section 2.4.2), and $\hat{P}_k$ describes the probability of capturing an image of an animal at the snapshot moment, within the camera field of view (FOV) and truncation distance (w), and is estimated by modelling the detection function using measured radial distances.

The same modelling assumptions as conventional distance sampling from observational point or line transects apply. Sampling localities are random and independent of animal distributions, animals are detected at their initial locations, distances are accurately measured, and detection probability at zero distance is certain (Buckland et al., 2001). However, in CTDS, violation of certain assumptions is expected, and caveats exist to minimise resulting bias. Animals passing near to the camera are likely to be missed due to moving out of the frame too quickly, passing below the camera, or being too close for species identification, resulting in fewer than expected detections at near distances. This can be addressed by deploying cameras at an appropriate height for target species, or applying left truncation (Buckland et al., 2001; Howe et al., 2017). Observations are also unlikely to be independent due to inclusion of multiple detections within the same capture occasion as the animal moves across the FOV. Violation of the assumption of independence introduces overdispersion and invalidates traditional model selection process using Akaike information criteria (AIC). To address this, Howe et al. (2019) proposed an alternative method for over-dispersed sampling data that estimates an over-dispersion factor ($\hat{c}$), calculated from the X^2 goodness-of-fit statistic divided by its degrees of freedom (QAIC; Howe et al., 2019).

2.4.2. Effort Calculations

In CTDS, sampling effort is obtained by defining a series of discrete ‘snapshot moments’, at which animals are considered available for detection, which aims to reduce bias in initial detection distances (Howe et al., 2017). Sampling effort is calculated at each survey site as: $e_k = \frac{\theta T_k}{2\pi t}$, with θ defined as the angle of camera view, T_k as the sampling period, and t (or effective t) as the interval between snapshot moments (Howe et al., 2017). In first iterations of CTDS, snapshot moments were deemed to be pre-determined *‘t’* units of time apart, initially defined as fixed second intervals in a video. However, this approach can significantly reduce the available data for density analysis when using bursts of still images from camera traps, as captures falling outside the snapshot moment are excluded. To address this, recent studies have proposed the use of an effective snapshot interval (effective *t*), based on camera trapping rates (Corlatti et al., 2020; Mason et al., 2022; McKaughan et al., 2023), which can increase the applicability of CTDS for less abundant populations, and allow flexibility in camera trap settings.

For use with sequences of still camera images, effective *t* has been defined as the minimum time between single-image captures (Corlatti et al., 2020), the mean time between photos in a burst (Mason et al., 2022; McKaughan et al., 2023), or the mean time between the combined duration of a burst and trigger interval (McKaughan et al., 2023). Sampling effort was estimated using two of the methods described in McKaughan et al. (2023): the trigger adjusted effort (TA) and the recovery-driven interval (RDI). Similar to approaches outlined in Corlatti et al. (2020) and Mason et al. (2022), the TA method defines effective t as the mean time between photos in a burst, calculated by dividing the burst time (B_k) by the number of images in a burst (n_k) and defining effective t as: $t = \frac{B_k}{n_k}$. The RDI method incorporates the burst time (B_k) and true trigger interval (R) to calculate a 'mean burst time' from which effective t is calculated as: $t = \frac{B_k + \mathrm{R}}{n_k}$ (McKaughan et al., 2023).

As camera performance metrics are likely to vary from the manufacturer's specifications (Corlatti et al., 2020), the true burst times and trigger intervals for each survey location were calculated directly from the capture data. The mean burst time for each site was extracted from the timestamp data of every capture event. The true trigger interval was determined from periods of time when cameras were triggered constantly during set up and removal, and verified by ex-situ testing, wherein cameras were triggered constantly for five minutes using different setting combinations and the timestamp of triggers extracted. In consideration of the expected variability in camera performance between different camera trap makes, and to allow for flexibility in camera settings between survey sites, effective *t,* and subsequently survey effort, was calculated on a site-specific basis. Periods of time where cameras were inactive due to battery failure or obstruction of the FOV were removed from T_k, and additional time cameras were inactive during trigger intervals was excluded from T_k when applying the TA method.

2.4.3. Activity

In CTDS, species are not considered available for detection during periods of inactivity. Therefore, the time cameras were active at each site (T_k) was adjusted based on species' temporal activity schedules derived from capture occasions during the study period. Using the 'activity' package in R (Rowcliffe et al., 2014), the timestamp from the first image in each trigger sequence was fitted to a flexible circular distribution, estimating the proportion of time each species was active in each study site from the fitted model distributions (Rowcliffe et al., 2014). To increase sample size available, all data captured from cameras deployed within the study area within the five-month period from June – November 2022 was included in activity analysis, including captures obtained from cameras deployed as part of a pilot study, and opportunistic captures from cameras deployed outside of the CTDS grid. Timestamps were adjusted for seasonal variation in daylight hours, and a bandwidth multiplier of 1.5 was applied to improve robustness (Rowcliffe et al., 2014). No time-to-independence filter was applied (Peral et al., 2022), but captures where species showed reactivity to the camera were excluded to avoid overestimation from repeated triggers (e.g. a clear change in direction, approaching or directly interacting with the camera). A coefficient of activity overlap (Δ) was calculated between the two black-backed jackal populations modelled using the overlap package in R with 1000 bootstrap repetitions (Ridout and Linkie, 2009).

2.4.4. Effective Detection Angles

Within calculations of survey effort (e_k), the proportion of a 360° circle covered by a camera traps FOV is represented by ($\frac{\theta}{2\pi}$), where θ represents the camera field of view. The FOV for each camera make was verified to be accurate against the handbook specifications using static object markers placed at variable distances from the camera trap. These markers were positioned at the widest point within the frame of images taken by the camera. By measuring the distance between these static markers, the angle of view could then be calculated using trigonometry. However, the effective angle at which animals are detected by camera traps may be narrower than the handbook specified FOV, as probability of detection decreases towards the periphery of the camera's frame. Therefore, for each camera trap make used in the survey, the effective detection angle was estimated for each modelled species, which was then incorporated into effort calculations as θ (Rowcliffe et al., 2011). As with availability for detection, this calculation included data from all camera traps deployed within the study area within the five-month period from June to November 2022, including captures obtained from cameras deployed as part of a pilot study, and opportunistic captures from cameras deployed outside of the CTDS grid.

Separating data captured by each camera trap make, the angle from the camera lens to the midpoint of the animal was recorded at the point of initial detection within each capture sequence. Using the respective camera model's FOV, the relative angle of capture was calculated, with 0° being at the vertical midline, and angles increasing towards the periphery of the frame. The relative angles of capture were then grouped into 0-20%, 20-60% and 60-100% bins, and fitted to a half normal detection function to estimate the effective detection angle using the Distance package in R (Hofmeester et al., 2017; Mason et al., 2022).

2.4.5. Density Estimation

All density estimates were modelled using the Distance package in R (Miller et al., 2019). A minimum of 60 observations was deemed sufficient for reliable density estimates (Buckland et al., 2001), and analytical decisions regarding truncation and heaping were based on exploratory analysis of histograms of radial distances for each modelled population. Data was binned based on visual inspection of the histograms of radial distances to eliminate bias from heaping (Buckland et al., 2001; Howe et al., 2017). Right truncation was applied to account for tailing, where greater than expected detections were recorded at far distances, and fewer than expected detections at low distances was addressed by left truncation at the distance of peak detection probability for each modelled population.

Captures where animals showed clear reactivity (i.e., clearly changing direction of movement in response to camera trap) or attraction to the camera were excluded from analysis to minimise bias in encounter rates. The remaining radial distances were fitted to detection functions and modelled using uniform with up to 3 cosine adjustments, half-normal and with up to 2 cosine, hermite and polynomial adjustments, and hazard-rate with up to 1 cosine, hermite and polynomial adjustments. Excluding models that were not naturally monotonically decreasing (Buckland et al., 2001), final model selection was based on two-step model selection procedure outlined by Howe et al. (2019) for over dispersed data (Buckland et al., 2001; Howe et al., 2017, 2019). Variance was estimated over 1000 bootstrap repetitions using resampling of points with replacement (Buckland et al., 2001).

3. Results

3.1. Camera Trap Survey Results

Across the two study sites, 82 camera trap surveys were conducted in 71 independent locations (Table 1; Figure 1a). Eleven sites were resampled due to battery failure or interference by wildlife, and data was included in analysis up until the point of failure.

18670 images of 35 different mammalian species of were recorded on SGR, and 9164 images of 23 species were recorded on the MUA (Appendix S1). Of the target mesocarnivore species, 910 images were captured: 556 on SGR and 354 on the MUA (Table 1). Using 60 records of radial distance measurements as a minimum for CTDS analysis (Buckland et al., 2001), density estimates were able to be modelled for brown hyaena on SGR, and black-backed jackal on both SGR and MUA.

Table 1. Survey capture data

Site	Survey locations	Surveys	Trap nights	*Images captured of target species*					
				BH	BBJ	Aard	BEFx	Car	HB
SGR	47	51	346.5	323	132	21	50	25	5
MUA	24	31	196	5	257	50	25	12	5

Survey locations is the number of independent locations surveyed; surveys is the number of surveys conducted including repeated samples. Trap nights is the number of active 24-hour cycles completed by independent cameras. Images captured of target species is the number of images with a distance measurement for each mesocarnivore; brown hyaena (BH), black-backed jackal (BBJ), aardwolf (Aard), bat-eared fox (BEFx), caracal (Car) and honey badger (HB).

3.2. Activity

The proportion of time each species spent active across the two study sites was similar (Table 2), and consistent with expected activity patterns for primarily nocturnal predators. Both species showing marginally higher proportion of active time on the MUA than SGR. Brown hyaena showed clear nocturnal activity pattern, whereas variability was observed between black-backed jackal on the two sites. On the MUA, black-backed jackal showed clear crepuscular peaks of activity, whereas this was less clear on SGR, with diurnal and extended nocturnal activity observed (Figure 4; $\Delta = 0.68$, 95% confidence interval 0.62 – 0.81).

Table 2. Availability for detection

Species	Site	n	Availability for detection	se	lcl	ucl
Black-Backed Jackal	SGR	56	0.400	0.082	0.302	0.602
Black-Backed Jackal	MUA	91	0.479	0.056	0.350	0.552
Brown Hyaena	SGR	72	0.306	0.043	0.224	0.402
Brown Hyaena	MUA	38	0.316	0.060	0.241	0.465

Site is Shamwari Private Game Reserve (SGR) or the mixed used agricultural area (MUA). 'n' is the number of data points included in activity analysis, including captures from extra-grid cameras, but excluding captures where animals reacted to the camera. Availability for detection is the proportion of time species are considered active, calculated from the fitted flexible circular distribution. Standard error (se), 2.5% lower confidence interval (lcl) and 97.5% upper confidence interval (ucl).

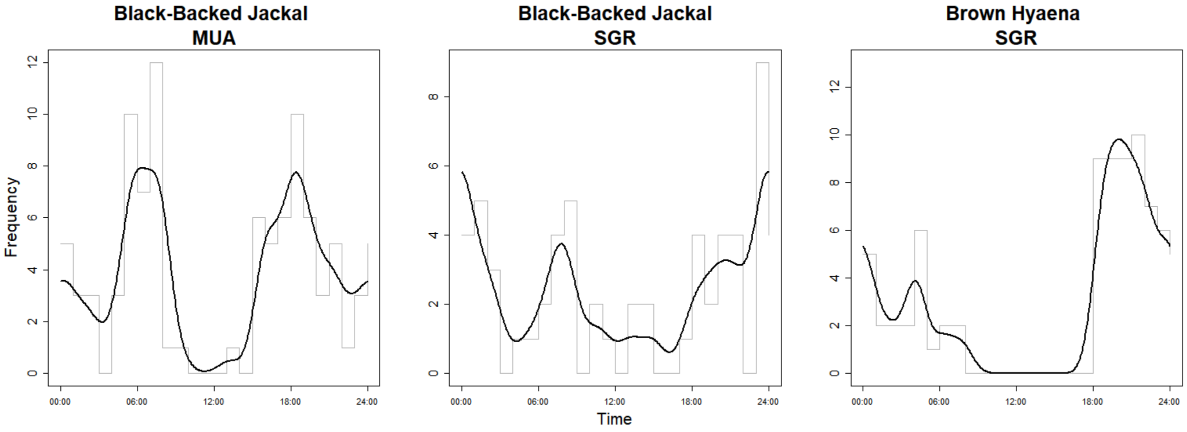

Figure 4. Activity schedules for mesocarnivores with sufficient captures to model density on Shamwari Private Game Reserve (SGR) and a mixed used agricultural area (MUA).

3.3. Effective Detection Angles

Unadjusted half normal were the best fitting for all effective detection angle models. Effective angle of detection for each camera make was similar for both species, and all but one model showed narrower effective detection angle than the camera specifications FOV (Table 3). Browning cameras have a wider handbook FOV than Bushnell cameras, and effective angle of detections were very close (>98%) or equal to the handbook specifications for both target species, indicating greater detectability at the edges of the FOV for the Browning than Bushnell camera traps.

Table 3. Effective detection angles

Species	Camera make	Handbook FOV (rad)	EDA (rad)
Black-Backed Jackal	Bushnell	0.663	0.499
Black-Backed Jackal	Browning	0.960	0.944
Brown Hyaena	Bushnell	0.663	0.566
Brown Hyaena	Browning	0.960	0.960

Handbook FOV is the field of view described in the manufacturer specifications in radians (rad). EDA is the species-specific effective detection angle for each camera trap make, included in effort calculations as angle of view (θ).

3.4. Camera Performance

3.4.1. Photographic Burst Times

Based on the manufacturer's specifications, variation in performance between Bushnell and Browning camera makes was expected. However, inconsistencies were also recorded in photographic burst time between individual camera units of the same make, and more surprisingly, between different surveys that used the same camera unit. The mean burst time recorded for each combination of settings varied considerably, particularly among the Browning camera units (Figure 5). As a result, using mean burst times to calculate effective *t* across all camera stations was unlikely to reflect the true survey effort, and so effort was calculated on a site-specific basis to reflect real camera trap performance metrics at each survey site (recorded values for effective *t* are shown in Appendix S2).

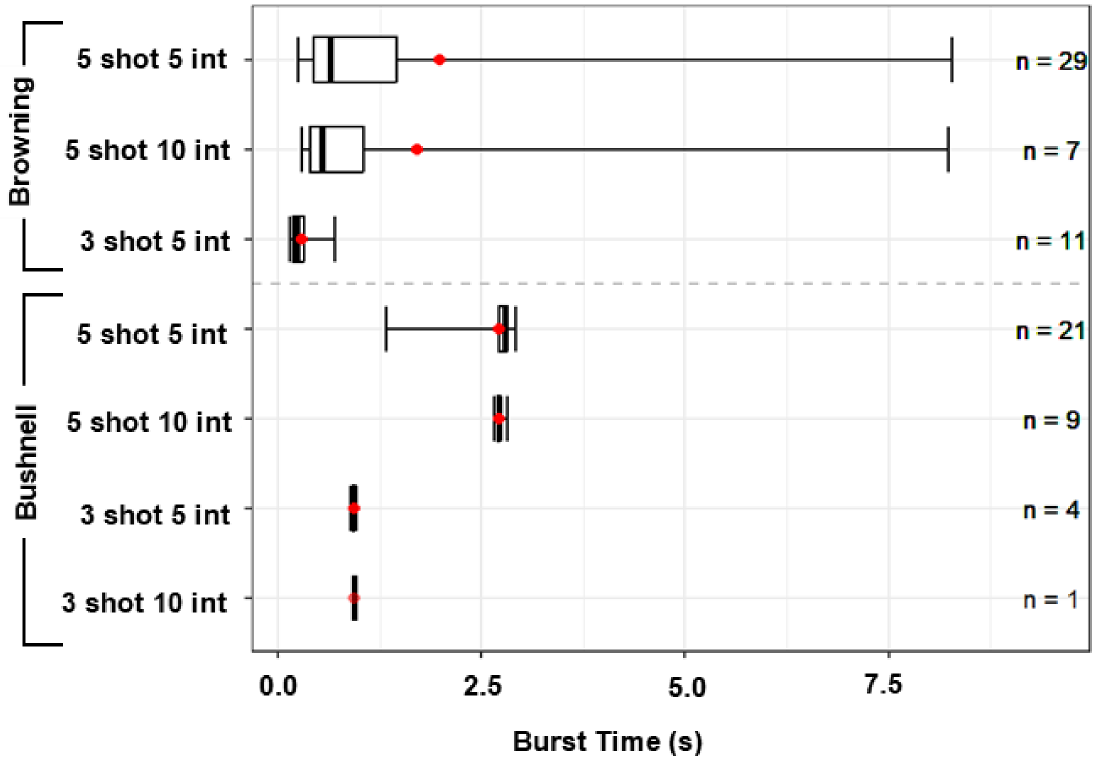

Figure 5. Burst times of camera traps units for each sampling occasion. Y axis: ‘shot’ refers to number of images in a burst; ‘int’ refers to the handbook trigger interval programmes on deployment of the camera trap. The box and whisker plot depicts distribution of camera trap burst times under different programmed setting combinations. ‘Box’ shows the interquartile range (IQR), with the median (50th percentile) shown as the bold line. ‘Whiskers’ extend to the minimum and maximum values. Red points indicate mean burst time for each setting. ‘n’ is the number of sites sampled with the specified settings.

3.4.2. Trigger Intervals

The trigger interval between bursts (minimum time taken for the camera trap to recover after triggering before a new trigger event can be captured) in ex-situ testing were consistent with those recorded within field surveys during periods of constant movement, but inconsistent with handbook trigger intervals (Table 4). Using the handbook trigger intervals in to calculate overall sampling effort would therefore have underestimated effort and resulted in positive bias in density estimates. As a result, the true trigger interval (*R*) for each camera deployment was incorporated into calculations of survey effort.

Table 4. Camera trigger interval tests

Camera Make	Handbook interval (s)	n shot	Real interval (s)
Bushnell	5	All	6
Bushnell	10	All	11
Browning	5	5	2
Browning	5	3	1
Browning	10	All	13

'Handbook' interval refers to the trigger interval that the camera trap was programmed to take between potential bursts, in seconds (s). 'n shot' is the number of images in a burst: 3, 5 or 'All' (when no difference in real interval was observed between 3 and 5 images in a burst). 'Real interval' (*R*) is the interval between the end of one capture and the start of the next.

3.5. Density Estimates

Left truncation was initially applied at the point of greatest probability of capture per unit area. However, it became necessary to relax this rule to retain maximum data for more robust model fitting, and truncation decisions were ultimately based on exploratory analysis of the histograms of radial distances for each modelled population and testing of model fit (Ruette et al., 2003; Mason et al., 2022). Right truncation was applied where there were higher than expected detections at far distances, usually as a result of the presence of a road or trail at within the camera detection zone.

Unadjusted hazard rate models were the best fitting for two of the three modelled population datasets, and hazard rate with 2 cosine adjustments was the best fitting for black-backed jackal within the MUA (Table 5). For both snapshot methods applied, density of black-backed jackal was estimated as marginally higher on the MUA (17 / 100 km^2 for TA and 97 / 100 km^2 for RDI) than SGR (16 / 100 km^2 for TA and 86 / 100 km^2 for RDI). For all modelled populations, the RDI snapshot method produced estimates than were over 5.5 times greater than those obtained using the TA snapshot method (Table 6). High coefficients of variation (CVs) were recorded, and this imprecision was mostly attributable to variance in encounter rate (Table 6). However, detection probability accounted for a larger proportion of variance for black-backed jackal on SGR than on the MUA, potentially reflecting greater spatial heterogeneity in capture events on the MUA (Appendix S3).

Table 5. Model parameters for density estimation of black-backed jackal (BBJ) and brown hyaena (BH) within Shamwari Private Game Reserve (SGR) and a mixed used agricultural area (MUA).

Species	Site	Detection locations	Truncation distance (m) (left - right)	Distance records	Model key	Adj. (order)	Effective detection radius (m)	Availability for detection
BBJ	MUA	13	1.5 - 15	251	Hazard Rate	Cos (2)	4.31	0.479
BBJ	SGR	17	1 - 15	123	Hazard Rate	-	3.63	0.400
BH	SGR	14	1 - 13	93	Hazard Rate	-	3.54	0.306

Detection locations is the number of camera sites where species were recorded. Distance records are number of radial distances included in model after truncation. Model key is the key function used to model detection probability, and Adj. (order) is the adjustment term and order of adjustment applied; cosine (cos) and no adjustment (-), Effective detection radius (m) is the distance at which the number of observations missed up to specified distance is equal to the number of observations beyond it. Availability for detection is the proportion of time spent active in a 24-hour period.

Table 6. CTDS density estimates for black-backed jackal (BBJ) and brown hyaena (BH) within Shamwari Private Game Reserve (SGR) and a mixed used agricultural area (MUA).

Species	Site	Snapshot method	Effort	Mean encounter rate	Encounter rate variance (%)	Detection probability variance (%)	$\widehat{D}$ / 100 km^2	Bootstrap			
								se	*lcl*	*ucl*	*cv*
BBJ	MUA	TA	21018387	1.19E-05	99.76	0.24	16.60	27512.99	4.95	26455.93	1566.797
BBJ	SGR	TA	16587618	7.42E-06	96.78	3.22	15.64	6200.10	2.97	23430.25	376.439
BBJ	MUA	RDI	3615321	6.94E-05	99.26	0.74	96.51	49885.15	26.33	26084.68	489.836
BBJ	SGR	RDI	3005571	4.09E-05	95.80	4.20	86.32	34029.00	21.93	138830.61	360.796
BH	SGR	TA	13208850	6.89E-06	96.27	3.73	11.77	2080.49	4.07	46.13	171.560
BH	SGR	RDI	2380083	3.82E-05	94.00	6.00	65.33	7525.42	23.72	233.07	115.271

Snapshot method refers to the method used to calculate snapshot intervals (TA = Trigger Adjusted Effort or RDI = Recovery Driven Interval) subsequently incorporated into effort calculations. Mean encounter rate is the mean number of observations per time. encounter rate variance and detection probability variance refer to the percentage of variance attributable to encounter rate and detection probability, respectively. Bootstrap data is based on 1000 repetitions: *se* = standard error, *lcl* = lower 95% confidence interval, *ucl* = higher 95% confidence interval, *cv* = percentage coefficient of variation.

4. Discussion

Mesocarnivore populations were surveyed from two adjacent properties: a protected game reserve (SGR), and a mixed-use agricultural area (MUA). Using CTDS, population density was estimated for black-backed jackal on both properties, and brown hyaena on SGR. Estimates varied according to the snapshot interval method applied, with the RDI method producing greater estimates than the TA method for all modelled populations. CVs were high for all estimates, and imprecision was almost entirely attributed to spatial heterogeneity in encounter rates. Here, I discuss the validity and precision of the density estimates and consider the methodological constraints regarding some of the key aspects of the CTDS and the approaches applied in this study.

4.1. Validity and Precision of results

4.1.1. Snapshot Approaches

Before discussing the validity of results, it is vital to consider the impact of the different snapshot approaches employed in this study in the context of their respective mathematical effect on estimated densities. The TA and RDI methods calculate effective *t* based on different combinations of camera trap performance metrics (see section 2.4.2). The TA method calculates effective *t* solely from burst time (B_k; $t = \frac{B_k}{n_k}$), whereas the RDI method incorporates trigger interval (*R*) into this parameter ($t = \frac{B_k + \mathrm{R}}{n_k}$). resulting in a higher value of *t*. Across all surveys, the mean value of effective *t* was 0.4 seconds (SE ± 0.04) using the TA method, increasing to 1.5 seconds (SE ± 0.11) for the RDI method, but there was considerable variation in the degree to which each method effected the output of effective *t* between surveys. A higher *t* effectively decreases survey effort, with subsequent larger density estimates produced (Table 6). As a result, density estimates derived from calculating *t* using the RDI method were more than 5 times greater than those obtained from the TA method.

This effect was also apparent in the original application of these snapshot approaches (McKaughan et al., 2023), where RDI produced significantly greater estimates than TA for mesocarnivore population densities in the Alldays region of Limpopo. McKaughan et al. (2023) reported considerably larger black-backed jackal densities using RDI than TA, with estimates exceeding any previously reported density within southern Africa. Congruent with the original publication of the method, this study found RDI population density estimates of brown hyaena to be implausibly high 65.3 /100 km^2 relative to previous estimates in similar environments, being over double that of the highest previous estimate within a protected area (Edwards et al., 2019; Table 7.1). As a result, density estimates derived from RDI snapshot methods are likely to overestimate density, and the TA method appears to be a more robust approach, having produced estimates within the expected range for many species (Mason et al., 2022; McKaughan et al., 2023). Further implications of the snapshot approaches employed and considerations around camera performance variability are discussed in section 4.2.1.

4.1.2. Density Estimates

Although relatively high compared to previous estimates (Table 7.1), the TA derived estimate of 11.8 brown hyaena / 100 km^2 was among the most precise of all modelled populations, and is comparable to densities reported in other small, fenced reserves (Welch and Parker, 2016; Edwards et al., 2019), as well as larger protected conservancies (Gush et al., 2022). Abundant carrion provisioning by apex predators likely contribute to this high density (Yarnell et al., 2013; Slater and Muller, 2014), in addition to the absence of a dominant competitor, spotted hyaena (Williams et al., 2021b). High densities can also be attributable to limited dispersal capability through impermeable boundary fences (Kesch et al., 2013). Although a degree of fence permeability is highly likely (Kesch et al., 2013; Williams et al., 2021a), previous studies of collared individuals have shown no cross-boundary movement of brown hyaena on SGR (Welch et al., 2016), and we recorded no overlap of individuals captured throughout the study period between the two study sites. Assuming impermeability of fence lines, individual territory sizes may be confined within SGR to avoid overlap with conspecifics, elevating population density. This highlights the potential for rapid population growth of brown hyaena on small, fenced reserves, and could be invaluable for population recovery by enabling provision of surplus individuals for translocation to extirpated areas (Welch and Parker, 2016), particularly given the near-threatened IUCN Red List status of brown hyaena (Wiesel, 2015). However, as this estimate was derived from a survey in a small section of SGR, it is likely that this density does not reflect the overall density of brown hyaena within the entire reserve, as habitat structure, intensity of human disturbance and density of apex predators are variable across the landscape, and impact localised population abundance.

Estimates of black-backed jackal densities using the TA method were low relative to previous estimates from populations around southern Africa on both SGR (15.6 / 100 km^2) and the MUA (16.6 / 100 km^2; Table 7.2). Estimates using the RDI method (96.5 / 100km^2 on the MUA and 86.3 / 100km^2 on SGR), are within the range of densities previously reported in the literature for this species (Table 7.2), but as previously discussed, these results should be interpreted with extreme caution as the RDI method appears likely to overestimate density (see section 4.1.1; McKaughan et al., 2023). Despite imprecision in estimates, there is a lack of reliable density estimates for black-backed jackal in southern Africa, and these results represent some of the few reported estimates outside of protected areas (Minnie et al., 2016).

One of the few reported estimates of black-backed jackal density outside of protected areas was from a commercial farming landscape in the Alldays area of Limpopo province, and applied CTDS with the same snapshot approaches used in this study (McKaughan et al., 2023). Greater density estimates were reported for black-backed jackal in the Limpopo study (29.8 - 46.2 / 100 km^2 [TA], 119.1 - 184.6 / 100 km^2 [RDI]) than found on the MUA (McKaughan et al. 2023; see Table 7.2). This is unsurprising given the differences in resource availability across the two regions, as greater landscape heterogeneity in the Limpopo study area likely supports greater foraging opportunities on properties managed for game and small stock farming (Klare et al., 2010; Drouilly et al., 2018), as well as crop production (Williams et al., 2019), favouring generalist mesocarnivores (Roemer et al., 2009; Clavel et al., 2011).

The estimate of 15.6 / 100 km^2 for black-backed jackal within SGR is also low relative to other protected areas; where densities of 37 / 100 km^2 have been reported in the Pilanesberg National Park (Yarnell et al., 2013), and 54.9 - 97.1 / 100 km^2 in Hwange National Park (Loveridge and Nel, 2013). This may be a result of the intensity of suppression from apex predators within SGR, as small private game reserves often exhibit high rates of population increase in lion (Miller and Funston, 2014; Welch et al., 2016). Furthermore, the removal of two subadult male lions from the SGR study area during the survey period indicates that the lion density of was high prior to this action (per comms with reserve management), which may account for observed low densities of black-backed jackal within SGR.

Table 7.1. Brown hyaena densities per 100 km^2 in protected areas

Reserve or region	Country	Method	Density	Citation
Welgevonden Private Game Reserve	South Africa	Camera Trapping SCR	2.8	Williams et al., 2021a
Songimvelo Game Reserve	South Africa	Camera Trapping SCR	2.8	Williams et al., 2021a
Pilanesberg National Park	South Africa	Telemetry	2.8	Thorn et al., 2009
Central Kalahari Game Reserve	Botswana	Track counts	2.9	Winterbach et al., 2017
Ithala Game Reserve	South Africa	Camera Trapping SCR	3.2	Williams et al., 2021a
Dinokeng Game Reserve	South Africa	Camera Trapping SCR	3.8	Williams et al., 2021a
Khamab Kalahari Reserve	South Africa	Camera Trapping SCR	5.3	Williams et al., 2021a
Venetia Limpopo Nature Reserve	South Africa	Camera Trapping SCR	5.6	Williams et al., 2021a
Lapalala Wilderness	South Africa	Camera Trapping SCR	8.5	Williams et al., 2021a
Kwandwe Private Game Reserve	South Africa	Camera Trapping SCR	8.7	Williams et al., 2021a
Central Tuli block	Botswana	Camera Trapping SECR	10.5	Vissia et al., 2021
Madikwe Game Reserve	South Africa	Camera Trapping SCR	9.5	Williams et al., 2021a
Wonderkop Nature Reserve*	South Africa	Camera Trapping SCR	10.1	Williams et al., 2021a
Pilanesberg National Park	South Africa	Camera Trapping SCR	10.7	Williams et al., 2021a
Zingela Nature Reserve*	South Africa	Camera Trapping SCR	10.8	Williams et al., 2021a
KwaZulu Private Game Reserve	South Africa	Camera Trapping SCR	11.4	Williams et al., 2021a
Shamwari Private Game Reserve	South Africa	CTDS	11.8	This study (TA)
Bubye Valley Conservancy	Zimbabwe	Camera Trapping SECR	14.7	Gush et al., 2022
Atherstone Nature Reserve*	South Africa	Camera Trapping SCR	15.1	Williams et al., 2021a
Kwandwe Private Game Reserve	South Africa	Camera Trapping	15.3	Welch and Parker, 2016
Okonjima Nature Reserve	Namibia	Camera Trapping	24.0	Edwards et al., 2019
Shamwari Private Game Reserve	South Africa	CTDS	65.3	This study (RDI)

Results of this study are shown in grey, with trigger adjusted (TA) and recovery drive interval (RDI) snapshot methods indicated. Protected sites that do not contain lion are indicated by an asterisk (*). Williams et al., 2021a estimates are derived from modelling approaches that considered fences impermeable.

Table 7.2. Black-backed jackal densities per 100 km^2

Reserve or region	Protection status	Country	Method	Density	Citation
Telperion Nature Reserve	Protected	South Africa	REM	2.0 - 5.0	Melville and Strauss, 2021
Skeleton Coast	Protected	Namibia	Strip Counts	7	Nel et al., 2013
Shamwari Private Game Reserve	Protected	South Africa	CTDS	15.6	This study (TA)
Mixed Use Farmland, Eastern Cape	Non-protected	South Africa	CTDS	16.6	This study (TA)
Commercial Farmland, Limpopo	Non-protected	South Africa	CTDS	24.8	McKaughan et al., 2023 (Hb)
Commercial Farmland, Limpopo	Non-protected	South Africa	CTDS	29.8	McKaughan et al., 2023 (TA)
Benfontein Game Farm	Protected*	South Africa	Telemetry Group Size	32.5	Klare et al., 2010
Giant’s Castle Nature Reserve	Protected	South Africa	Telemetry	35.0 - 40.0	Rowe-Rowe, 1982
Commercial Farmland, Limpopo	Non-protected	South Africa	CTDS	36.5	McKaughan et al., 2023 (Hb)
Pilanesberg National Park	Protected	South Africa	Line Transect Distance Sampling	37.0	Yarnell et al., 2013
Rooipoort Nature Reserve	Protected*	South Africa	Relative Abundance	42.9	Klare et al., 2010
Commercial Farmland, Limpopo	Non-protected	South Africa	CTDS	46.2	McKaughan et al., 2023 (TA)
Serengeti National Park	Protected	Tanzania	Transect Counts	50.0	Waser, 1980
Hwange National Park	Protected	Zimbabwe	Not specified	54.0 – 97.0	Loveridge and Nel, 2013
Shamwari Private Game Reserve	Protected	South Africa	CTDS	86.3	This study (RDI)
Mixed Use Farmland, Eastern Cape	Non-protected	South Africa	CTDS	96.5	This study (RDI)
Mankwe Wildlife Reserve*	Protected	South Africa	Line Transect Distance Sampling	115.2	Yarnell et al., 2013
Commercial Farmland, Limpopo	Non-protected	South Africa	CTDS	119.1	McKaughan et al., 2023 (RDI)
Commercial Farmland, Limpopo	Non-protected	South Africa	CTDS	184.6	McKaughan et al., 2023 (RDI)
Sandwich Harbour	Protected	Namibia	Strip Counts	291.0	Nel et al., 2013
Cape Cross	Protected	Namibia	Strip Counts	1305.0	Nel et al., 2013

Results of this study are shown in grey. Protected sites that do not contain lion are indicated by an asterisk (*). Snapshot methods used in this study and McKaughan et al. (2023) are indicated: trigger adjusted (TA) and recovery driven interval (RDI), in addition to handbook interval (Hb) method based on defining snapshot moments according to discrete seconds intervals (e.g. t = 1s), as described in original CTDS approach outlined by Howe et al. (2017).

4.1.3. Land Use Comparison

Although there is likely to be a degree of fence permeability between the MUA and SGR, the modelled mesocarnivore populations on each study site were considered discrete due to thorough fence inspection and maintenance, as well as previous findings of no trans-boundary movement of collared brown hyaena on SGR (Welch et al., 2016).

Black-backed jackal population densities were compared between the protected SGR and non-protected MUA study sites, with slightly higher densities recorded on the MUA than on SGR, regardless of the snapshot approach applied. However, these estimates were extremely imprecise with significant overlap in confidence intervals, making it difficult to infer meaningful conclusions regarding relative abundances on each property (Table 6). Higher estimates outside of the protected area would be unsurprising considering the lack of top-down control by apex predators outside of the reserve (Prugh et al., 2009). Additionally, periodic hunting on the MUA may contribute to elevated densities, as compensatory breeding responses, reduced reproductive suppression of subordinate individuals and immigration into vacant territories have been shown to cumulate in increasing local populations (Nattrass and Conradie, 2013; Wielgus and Peebles, 2014; Minnie et al., 2016).

Comparison between densities of brown hyaena between the two study sites was not possible due to insufficient captures on the MUA, which is likely a reflection of a low population density. It is expected that brown hyaena densities are higher on a protected area where carrion provisioning by hunting activities of large carnivores provide ample scavenging opportunities (Yarnell et al., 2013; Slater and Muller, 2014). While black-backed jackal are also known to scavenge carrion from larger predators, there is disagreement as to whether carrion provisioning influences black-backed jackal diet (Brassine and Parker, 2012; Yarnell et al., 2013), and previous dietary analysis on SGR has indicated limited scavenging behaviour of the black-backed jackal population within the reserve (Forbes, 2011). This suggests that apex predators do not provide the same ecological benefit to black-backed jackal that is observed in brown hyaena on SGR, congruent with prior investigations in the Northern Cape that reported a comparable facilitative and suppressive effect of apex predators on these mesocarnivore species (Yarnell et al., 2013).

The suppressive effect of lion on black-backed jackal population abundance is further supported by analysis of activity patterns, wherein a peak activity time for black-backed jackal around 00:00 was observed within SGR, as opposed to a strongly crepuscular pattern in the MUA (Figure 4). The noctural activity patterns of black-backed jackal within SGR can be explained by avoidance of the crepuscular peak active time of lions (Hayward and Hayward, 2007; Appendix S4). However this is unlikely to explain the diurnal activity of black-backed jackal observed within SGR that was not reflected in popualtions on the MUA (Figure 4). Considering the evidence for limited scavenging behaviour of black-backed jackal within SGR (Forbes, 2011), it is unlikely that individuals are more active during the day to exploit scavenging opportunities provided by lions in SGR (Fourie et al., 2015; Minnie, 2016). Lower levels of human activity on SGR may account for the difference in diurnal activity between the two populations, as black-backed jackal have been found to be less active during the day in areas of higher human persecution and disturbance (Hiscocks and Perrin, 1988; Kaunda, 2000; Kitchen et al., 2000; Green et al., 2022). However, further research into the degree of temporal avoidance observed in mesocarnivores in response to both intraguild and anthropogenic pressures is required to validate this assumption (Du Plessis et al., 2015). Furthermore, additional factors can influence black-backed jackal activity patterns (Ferguson et al., 1988; Kaunda, 2000; Botha et al., 2022; Wallin, 2022), thorough investigation of which was beyond the scope of this study.

The relative density estimates and variable patterns of temporal activity between the two populations of black-backed jackal on the MUA and SGR reveal how differential pressures can influence behaviour and density across different land uses. Although imprecision in estimates limits meaningful inferences that can be made about relative mesocarnivore densities from the results of CTDS analysis, temporal activity analysis reveals distinct patterns of behaviour that reflect differential pressures on each population.

4.2. Methodological Considerations

4.2.1. Site-Specific Snapshot Intervals

Our analysis of camera trap performance supported previous findings of inconsistencies between handbook specifications and real performance metrics (Corlatti et al., 2020; Mason et al., 2022; McKaughan et al., 2023), highlighting the importance of evaluating performance when applying CTDS. Inconsistencies were identified between the true duration of trigger intervals and those stated in the handbook specifications (Table 4), and variable burst times were recorded not only between camera trap makes, but also individual units (Figure 5). These inconsistencies are speculated to be due to remaining battery level, unit age or condition of the camera trap. Consequently, calculating effective *t* based on mean performances of all surveys may underestimate survey effort for units with shorter burst times, and overestimate survey effort for those with longer burst times. By calculating snapshot intervals on a site-specific basis, variation in camera trap performance between surveys can be identified and accounted for to determine overall sampling effort more accurately. Due to non-uniform camera trap settings across survey sites, comparison of site-specific versus survey-mean snapshot intervals was not possible. Snapshot intervals based on mean performance of camera traps with the same settings combinations (i.e. number of images in a burst and interval duration) were considered (Appendix S6), but the site-specific approach was considered to produce more accurate reflection of survey effort given the variation in camera performance metrics between sample sites. Furthermore, density estimates were not considerably different using this approach, and imprecision was still high (Appendix S6). Further empirical testing of the impact of this approach should be undertaken to evaluate the impact of site-specific snapshot interval calculations on density estimation and variance.

A key advantage of site-specific snapshot intervals is the inclusion of a broader range of camera trap units in monitoring efforts, regardless of variation in performance, setting limitations or angle of detection of units. In this study, two camera trap units of different makes were utilised (Bushnell Single Core 119938C; Browning Recon Force Extreme BTC-7FHD-PX), between which significantly different effective detection angles were measured. Site-specific intervals allowed us to account for this disparity, as well as variation in camera trap performance. While using uniform camera trap models may be logistically preferable due to standardised detectability, site-specific snapshot calculations can increase the pertinence of CTDS for population monitoring when researchers have limited resources available. Furthermore, this approach can reduce the impact of common problems associated with camera trapping. For example, frequent false detections of vegetation or non-target species (i.e. livestock) regularly result in battery failure or memory card saturation between site visits (Cusack et al., 2015b; Swanson et al., 2015; Jumeau et al., 2017; Meek et al., 2019; Mason et al., 2022), undermining density estimation by shortening survey effort in habitats with greater risk of repeated false triggers. Site-specific snapshot intervals can reduce the impact of these issues by allowing researchers to customise camera trap settings based on individual survey site characteristics, conserving battery life and ensuring continuous sampling between site visits.

Although logistically beneficial, the use of variable settings between study sites can significantly impact results when using different snapshot methods to calculate survey effort in CTDS. Due to incorporation of trigger intervals, the RDI method produced effective t values that were, on average, 6.3 times greater than those obtained using the TA method at the same survey site. The mathematical impact of increasing effective t is to effectively decrease survey effort, which subsequently elevates density outputs. Camera traps programmed to have longer trigger intervals resulted in significantly larger (up to 45.8 times) effective t values when calculated using the RDI method than the TA method, while camera traps with very short trigger intervals recorded only slight differences (Appendix Table S2). Similarly, rapid burst times and short burst sequences at some survey sites resulted in extremely low effective t

using the TA method (t = 0.05 - 0.38, as opposes to RDI: t = 1.66 - 4.25), which may have overestimated effort and resulted in negative bias in TA-derived estimates. Future application of CTDS using trigger-adjusted snapshot intervals should aim to use larger numbers of images in a burst to avoid negative bias from extremely low effective t. However, when shorter burst sequences are preferred or necessary, incorporating trigger intervals into snapshot interval calculations through the RDI method could mitigate the negative bias resulting from shorter burst times, but this remains to be tested.

4.2.2. Encounter Rate Variability

Encounter rate variance is considered the most prevalent source of variance in CTDS (Fewster et al., 2009; Howe et al., 2017), and spatial heterogeneity in encounter rates was responsible for most of the imprecision in this study (Appendix S2). This effect was primarily attributable to bias from the presence of fine-scale habitat features within the camera FOV, as a high number of capture events were recorded at sites with roads, game trails or fence lines, known to be preferentially used by many carnivore species (Mann et al., 2015; Cusack et al., 2015b, Swanepoel et al., 2016; Tamwar et al., 2021). Random camera placements coincidentally occurring on roads or game trails are considered unlikely to cause significant bias in estimates, providing they have not been intentionally targeted and are sampled in proportion to their occurrence within the landscape (Buckland et al., 2010). However, there is evidence to suggest that random camera placement may have underestimated population density of brown hyaena on the MUA study site, as capture rates from camera traps deployed on roads and trails were higher than those captured within the CTDS camera survey grid. At least two individuals were identified on the MUA by opportunistic cameras, whereas only one brown hyaena was captured on the property within the grid survey. This may be a result of few sampling locations, and the effect of bias from fine scale habitat features may be alleviated by increasing the number of survey locations (Cappelle et al., 2021). Lower CVs recorded for populations modelled on SGR could be indicative of the greater number of sampling locations and trap nights reducing imprecision from encounter rate variance on SGR than the MUA (Table 1). However, McKaughan et al. (2023) found no improvement in precision when using a migrating grid with more sample sites, deployed for shorter durations, compared to a static grid. For maximising the value of CTDS derived density estimates, future studies should aim to investigate ways survey design can improve precision in estimates, particularly regarding reducing the impact of encounter rate variance caused by significant spatial heterogeneity in capture events.

Considerable challenges were also encountered during fieldwork regarding camera placement due to a distinctive and characteristic lack of trees or other stable natural mounting points in the study region. Although some deviation from points is expected and unlikely to bias estimates (Howe et al., 2017), practical difficulties led to many instances of extreme deviation of camera placement from the pre-determined points. Although efforts to ensure displaced cameras were placed in similar habitats to the original point location, alternative camera placements may have inadvertently increased capture rates of species that preferentially use small-scale landscape features where cameras could be mounted, such as trees or fence lines, leading to positive bias in encounter rates (Kolowski and Forrester, 2017; Nattrass et al., 2017; Mason et al., 2022). Evaluating how localised site characteristics and camera displacements can cause bias and impact the validity and precision of results should be further investigated in future applications of CTDS.

Encounter rate variability remains the primary contributing factor to imprecision in CTDS, and key limitation of the method's efficacy for estimating densities with sufficient confidence to inform management decisions, particularly for species that exhibit strong spatial trends (Fewster et al., 2009; Palencia et al., 2021a). Adaptations of CTDS have achieved greater precision when modelling encounter rates as a function of environmental predictors (Delisle et al., 2023), which additionally improves applicability of CTDS to make population interferences over large scales or for heterogeneously distributed species (Mason et al., 2022). Stratified sampling designs have also been suggested to reduce sampling bias and increase precision when using traditional distance sampling or other unmarked density estimation methods (Fewster et al., 2009; Foster and Harmsen, 2012), although this remains to be tested on CTDS. Further development and evaluation of CTDS may provide insight into ways in which study design may reduce bias and uncertainty in estimates.

4.2.3. CTDS for Multi-Species Surveying

The ability of CTDS to estimate densities of multiple species within one survey is highly advantageous for large scale population monitoring (Bessone et al., 2020; Mason et al., 2022; McKaughan et al., 2023). However, species and population level variation in parameters included in CTDS can significantly influence density outputs, and applying uniform analytical decisions across multi-species or comparable population surveys may invalidate results. Left truncation distance is one such challenge to consider, applied in CTDS to account for few detections at short distances due to animals passing below or too close to the camera (Howe et al., 2017). Left truncation distance must be considered carefully, as removing data points outside of truncation distances affects how the slope of the probability detection function is extrapolated to zero. Left truncating at the lower 20% of captures has been recommended (Buckland et al., 2001), but this may be inappropriate for all species. For example, smaller, or faster moving species are more likely to pass below the camera field of view undetected, resulting a larger blind spot at shorter distances than for larger species. Although left truncation decisions were initially applied at the distance at which detection probability peaked for each species (Ruette et al., 2003; Mason et al., 2022), this rule had to be relaxed due to small sample sizes available, and left truncation was ultimately applied based on exploratory analysis of data distributions and testing model fit. As a result, left-truncation distances were lower than expected, which may have overestimated proportion of captures at close distances and potentially introduced negative bias in estimates (Buckland et al., 2001).

Differential responses to novel stimuli can also induce bias in density estimates using CTDS (Buckland et al., 2001), which can vary considerably between species and populations. For example, brown hyaena are known to frequently inspect or damage camera traps (Apps and Mcnutt, 2018; McKaughan et al., 2023), and despite removing images where reactivity to the camera was evident, low effective detection distances and a greater contribution of detection probability variance to overall variance are likely indicative of an attraction towards cameras, potentially contributing to upward bias in density estimates (Table 6; Apps and Mcnutt, 2018). Bias in density estimates can also occur from differential population responses to novel stimuli as a result of learned behavioural adaptations towards anthropogenic activities. A higher proportion of variance was attributed to detection probability for the black-backed jackal population on SGR than the MUA, potentially indicating a lesser negative response to novel stimul (i.e. camera traps) on the protected landscape than on the farmland where populations have been subject to persecution (Nattrass et al., 2017).

In consideration of the anthropogenic threats experienced by black-backed jackal populations on the MUA study area in the past, it is conceivable that individuals in this study site exhibit greater vigilence in response to novel stimuli which would account for lower proportion of variance attributed to detection probability than on SGR. The patterns of temporal activity patterns of black-backed jackal across the two study sites also reflect this, showing evidence of temporal avoidance of humans on the MUA that was not mirrored in the SGR population (Figure 4; see section 4.1.3). Reduced vigilance towards anthropogenic stimuli within protected areas will likely increase instances of attraction to the camera traps, potentially resulting in positive bias in encounter rates and greater loss of data due to reactivity. Furthermore, as animals are only considered available for detection when they are active in CTDS, temporal availability for detection is used to adjust the total duration camera traps were active at each site (T_k). Therefore, consideration of population-level responses to different land uses and anthropogenic pressures should be considered when applying CTDS, particularly for species that demonstrate high behavioural plasticity.

Inability to monitor multiple species populations is a key limitation of capture—mark recapture (CMR) density estimation techniques, and practical limitations of these methods may limit their application in some areas. CMR methods using camera traps rely upon obtaining sufficient captures of individuals that can be clearly identified, which often depends on using camera models with white or xenon flash to provide high quality images (Rovero and Zimmerman, 2016). This approach is often unfavourable for use on small, private game reserves, as the conspicuous presence of cameras may be undesirable for tourist operators. Furthermore, high visibility flash cameras are more disruptive to wildlife and may fail to obtain sufficient captures for ‘trap-shy’ species or populations (Wegge et al., 2006; Rovero et al. 2013; Meek et al. 2014). Using cameras with low, or no-glow flash settings on camera traps is recommended for CTDS to reduce bias from animals reacting to the camera, and therefore may be more applicable to use on protected areas where minimising disruption to tourists and wildlife is a priority (Ehlers Smith et al., 2018). CTDS also has the advantage of being able to utilise all captured images where species can be identified, regardless of image quality, increasing applicability to faster moving or less abundant populations, in addition to allowing simultaneously surveying of multiple marked and unmarked species, increasing efficiency of monitoring.

5. Conclusion

Despite high imprecision, the densities reported here are some of the few available estimates for southern African mesocarnivores, particularly outside of protected areas, and offer insight into mesocarnivore population statuses on protected and non-protected private landscapes in the Eastern Cape of South Africa. Density estimates revealed variable responses of species and populations according to distinct anthropogenic and interspecific pressures, which have implications for conservation and management of populations.

Small private game reserves can be vital contributors to national population recovery of threatened species, such as brown hyaena (Child et al., 2016; Wiesel, 2015), However, effective and continuous monitoring of species perceived to be a threat to people or livelihoods outside of protected areas must be implemented on small, fenced reserves to avoid negative interactions emerging should individuals transverse fences (Wiesel, 2015; Lindsey et al., 2013; Thorn et al., 2015; Banasiak et al., 2021a; Whitehouse-Tedd et al., 2021). While working landscapes have the potential to support mesocarnivore populations, high imprecision in densities reported in this study make drawing conclusions about relative abundances or landscape level impacts on densities challenging. Additionally, the MUA study site covered a small area and relatively homogenous land use, and therefore fails to offer insight into broad scale population densities across the range of working landscapes in the region. Expansion of the study to include multiple properties would allow insight into the impact of different land uses and anthropogenic pressures on mesocarnivore populations, improving our knowledge of the drivers of mesocarnivore densities and identifying key conservation and management challenges in this region.

Camera trapping methods to estimate population densities of unmarked species can present a cost efficient and robust system to monitor populations of multiple species simultaneously, and testing of these methods under different scenarios and environmental contexts is vital to ensure the level of precision achieved offers meaningful ecological insight. Validation and development of CTDS can enable managers to make evidence-based decisions regarding population management to ensure continued ecological integrity and human-wildlife coexistence. The site-specific approach to defining snapshot intervals demonstrated in this study highlights the potential for flexibility in CTDS study design, potentially allowing the method to be incorporated into established, ongoing game monitoring regimes within protected areas. While CTDS has the potential to allow widespread and concurrent monitoring of multiple species on a range of landscapes, population and species level variation should be considered in future application, and further design-based testing of is required to improve precision. Future studies should aim to evaluate CTDS against known population sizes or established density estimation techniques to further validate results.

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Appendix S1. Mammalian Captures by Study Site

Species	SGR	MUA
Carnivores	5194	357
Aardwolf	21	50
Bat-Eared Fox	50	25
Black-Backed Jackal	**132**	**257**
Brown Hyaena	**323**	5
Caracal	25	12
Honey Badger	5	5
Large Spotted Genet	27	▨
Lion	4577	▨
Meerkat	28	3
Mongoose	88	84
Striped Polecat	33	8
Naturally occurring game	1750	6545
Aardvark	19	30
Bushbuck	431	26
Bushpig	40	▨
Common Duiker	454	1124
Common Warthog	367	1222
Greater Kudu	57	1715
Mountain Reedbuck	15	1836
Porcupine	50	169
Steenbok	57	5
Waterbuck	260	418
Stocked Game	11460	793
African Buffalo	788	▨
Black Wildebeest	220	▨
Blesbok	▨	777
Common Eland	80	▨
Elephant	492	▨
Giraffe	154	▨
Impala	3259	▨
Nyala	5	▨
Red Hartebeest	188	▨
Sable	10	▨
Zebra	6264	16*
Primates	83	512
Chacma Baboon	73	512
Vervet Monkey	10	▨
Grand Total	19769	15190

Shamwari Game Reserve (SGR) and a mixed-use agricultural area (MUA). Numbers indicate total images captured, not individual capture occasions. Modelled species shown in **bold.** Small mammals and livestock not included. Naturally occurring game includes species that may have colonised the MUA from adjacent game reserves but now have an unmanaged breeding population. Grey squares indicate no captures. *****Zebra captured on MUA was confirmed to have moved through the fence from a neighbouring property.

Appendix S2. Variable Settings and Effective *t* at Camera Stations

						Snapshot Interval (effective *t*)	
Station ID	Site	Camera Make	Camera ID	Number of images in burst (B_k)	Trigger interval (Handbook)	TA	RDI
MA1	MUA	BROWN	30	5	5	0.05	0.38
MA2	MUA	BUSH	12	3	5	0.12	0.45
MA3	MUA	BROWN	5	5	5	0.55	2.75
MA4	MUA	BUSH	7	5	10	0.56	2.76
MA5	MUA	BUSH	7	5	10	0.11	2.71
MA6	MUA	BROWN	6	5	10	0.55	1.75
MA7-1	MUA	BROWN	30	3	5	0.05	0.45
MA7-2	MUA	BUSH	8	5	5	0.10	0.50
MA8-1	MUA	BROWN	17	3	5	0.58	1.78
MA8-2	MUA	BROWN	3	5	5	0.05	0.45
MA9	MUA	BROWN	6	5	5	0.23	0.57
MA10	MUA	BUSH	11	5	5	0.06	0.39
MA11	MUA	BROWN	9	3	5	0.06	0.39
MA12-1	MUA	BROWN	3	3	5	0.06	0.40
MA12-2	MUA	BUSH	12	5	5	0.07	0.41
MA13	MUA	BUSH	1	5	5	0.08	0.41
MA14-1	MUA	BROWN	29	3	5	0.09	0.49
MA14-2	MUA	BUSH	7	3	10	0.57	1.77
MA15-1	MUA	BROWN	10	3	5	0.55	1.75
MA15-2	MUA	BROWN	6	5	10	0.09	0.42
MA16	MUA	BUSH	7	5	10	0.09	0.43
MA17	MUA	BROWN	29	3	5	0.57	1.77
MA18	MUA	BROWN	9	3	5	0.06	2.66
MA19-1	MUA	BUSH	2	3	5	0.54	2.74
MA19-2	MUA	BROWN	5	5	5	0.10	0.50
MA20-1	MUA	BROWN	4	3	5	0.23	0.63
MA20-2	MUA	BROWN	6	5	5	0.57	1.77
MA21	MUA	BUSH	8	5	5	0.33	0.73
MA22	MUA	BROWN	29	5	5	0.11	0.51
MA23	MUA	BROWN	5	5	5	0.15	0.49
MA24	MUA	BROWN	9	3	5	0.15	0.55
SH16	SGR	BROWN	9	3	5	0.54	1.74
SH17	SGR	BUSH	13	5	5	0.16	0.56
SH18	SGR	BROWN	3	5	5	0.30	2.30
SH19	SGR	BUSH	2	5	5	0.56	1.76
SH20	SGR	BUSH	2	3	5	0.31	3.98
SH21	SGR	BROWN	17	5	5	0.31	2.31
SH22	SGR	BUSH	2	5	5	0.31	2.31
SH23	SGR	BROWN	17	5	5	0.32	2.32

SH24	SGR	BUSH	11	5	5	0.06	0.46
SH25	SGR	BUSH	13	5	5	0.56	1.76
SH26	SGR	BUSH	11	5	5	0.26	1.46
SH27	SGR	BUSH	2	5	10	0.56	1.76
SH30-1	SGR	BUSH	7	5	10	0.54	2.74
SH30-2	SGR	BROWN	4	5	5	0.53	2.73
SH31	SGR	BROWN	17	5	10	0.30	0.70
SH32	SGR	BROWN	10	5	5	0.29	2.89
SH33	SGR	BROWN	29	5	5	1.58	1.98
SH35	SGR	BROWN	18	5	5	0.05	0.45
SH36	SGR	BUSH	1	5	5	0.29	0.69
SH37	SGR	BUSH	8	5	5	0.56	1.76
SH38	SGR	BROWN	3	5	5	0.56	1.76
SH39	SGR	BROWN	10	5	5	0.07	0.47
SH40	SGR	BROWN	4	5	5	1.66	2.06
SH41-1	SGR	BUSH	12	5	5	0.18	0.58
SH41-2	SGR	BROWN	17	5	5	0.55	1.75
SH42	SGR	BROWN	6	5	10	0.11	0.51
SH43	SGR	BROWN	10	5	5	0.06	2.66
SH44	SGR	BROWN	18	5	5	1.60	2.00
SH45-1	SGR	BROWN	30	5	10	0.08	0.48
SH45-2	SGR	BROWN	30	5	5	0.09	2.69
SH46	SGR	BROWN	4	5	5	0.10	0.50
SH47	SGR	BROWN	4	5	5	0.11	0.51
SH48	SGR	BUSH	13	5	5	0.07	0.47
SH49	SGR	BUSH	12	5	5	0.54	1.74
SH50	SGR	BUSH	11	5	5	0.57	1.77
SH51	SGR	BROWN	10	5	10	0.55	1.75
SH52	SGR	BUSH	11	5	5	1.65	4.25
SH53	SGR	BROWN	10	5	5	0.53	1.73
SH54	SGR	BROWN	3	5	10	1.60	2.00
SH62	SGR	BROWN	17	5	5	0.13	2.73
SH63	SGR	BROWN	30	5	5	0.13	0.53
SH64	SGR	BUSH	1	5	5	0.28	0.68
SH65-1	SGR	BUSH	13	5	5	0.56	1.76
SH65-2	SGR	BROWN	10	5	5	0.54	1.74
SH66	SGR	BUSH	12	5	5	1.66	2.06
SH67	SGR	BUSH	8	5	10	0.54	1.74
SH79	SGR	BUSH	1	5	10	0.54	2.74
SH8	SGR	BROWN	5	5	5	0.54	2.74
SH80	SGR	BUSH	1	5	10	0.29	0.69
SH81	SGR	BUSH	12	3	5	0.56	2.76
SH82	SGR	BUSH	8	5	10	0.54	2.74

BUSH = Bushnell Single Core 119938C; BROWN = Browning Recon Force Extreme BTC-7FHD-PX Snapshot Interval: TA = Trigger Adjusted Effort, RDI = Recovery Driven Interval. Repeated surveys are indicated by ‘-#’.

Appendix S3. Encounter Rates of Sampling Locations

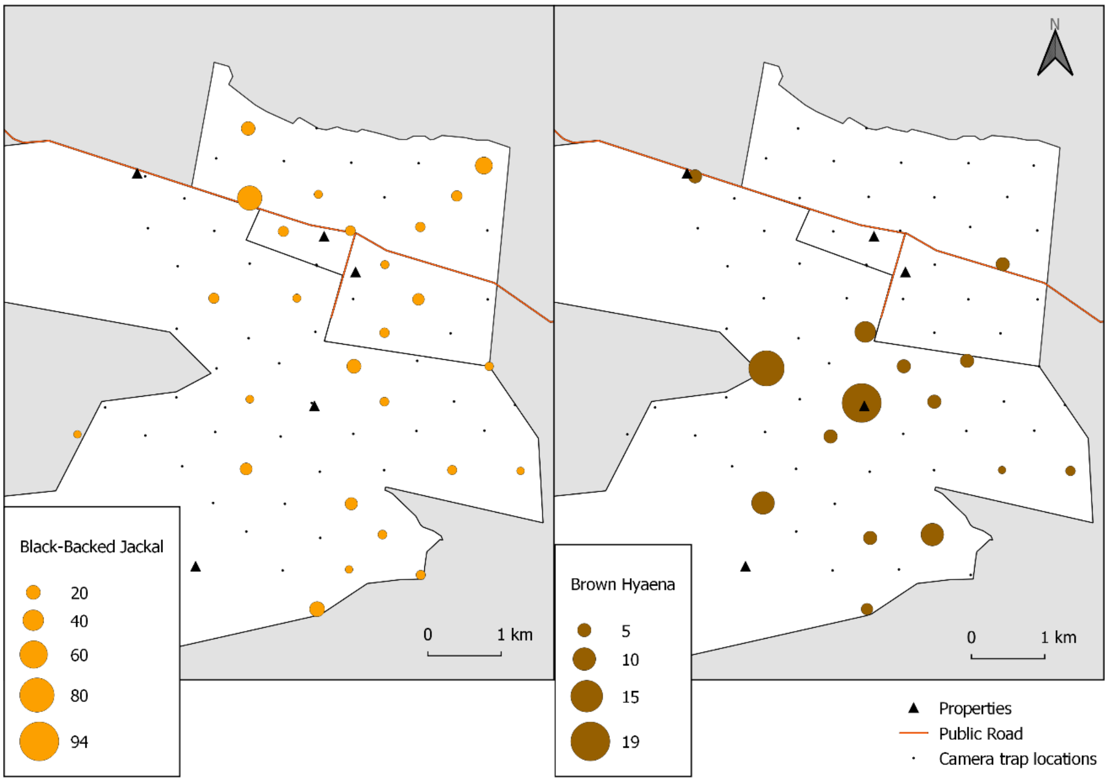

Figure S3. Number of images obtained of target species at each camera trap location. Increasing circle diameter reflects increasing number of images captured at that camera trap site. Captures from resampled locations are combined. Camera trap locations with < 1 detections are indicated by a black dot. Properties include commercial lodges and private residences.

Appendix S4. Activity Overlap

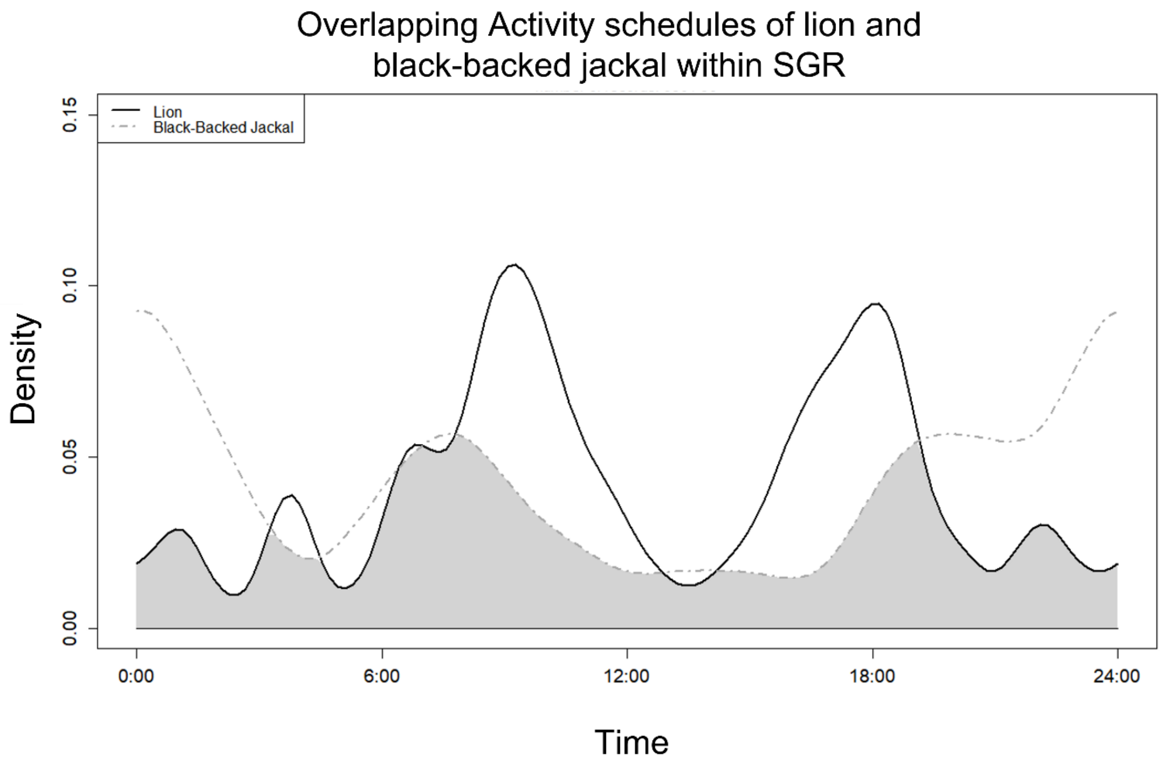

Figure S4. Activity overlap between lion and black-backed jackal on Shamwari Private Game Reserve (SGR) demonstrates crepuscular activity patterns of lion and prolonged diurnal activity of black-backed jackal, suggesting a degree of temporal partitioning. Overlap coefficient (Δ) = 0.62.

Appendix S5. Detection Probability and Probability Density Functions

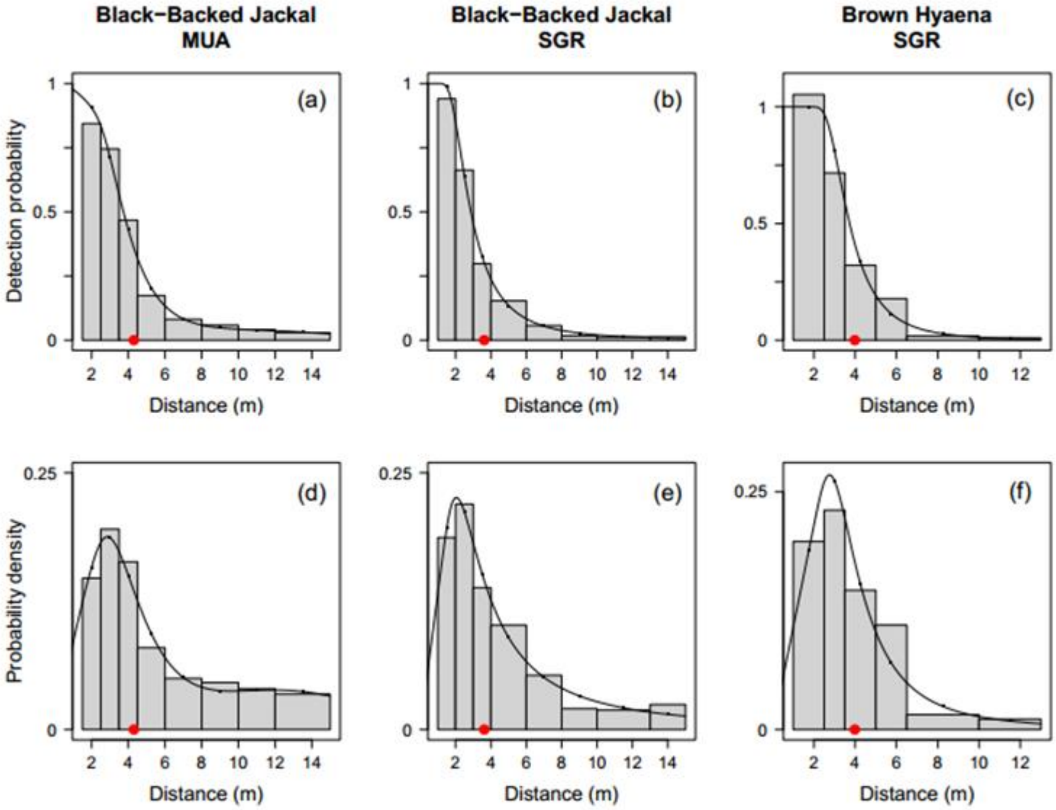

Figure S5. Histograms of detection probability (top) and probability density function of observed radial distances (bottom) for captures of black-backed jackal on MUA (left) and SGR (middle) and for brown hyaena on SGR (right). Red dot indicates effective detection radius.

Appendix S6. Density estimates derived from site-specific versus setting-mean snapshot intervals (effective t)

Species	Site	Snapshot method	**Site Specific *t***		**Setting Mean *t***	
			$\hat{D}$ / 100 km^2	*cv*	$\hat{D}$ / 100 km^2	*cv*
BBJ	MUA	TA	16.60	1566.797	20.20	919.808
BBJ	SGR	TA	15.64	376.439	16.78	444.952
BBJ	MUA	RDI	96.51	489.836	97.80	389.775
BBJ	SGR	RDI	86.32	360.796	74.30	295.246
BH	SGR	RDI	65.33	115.271	56.48	73.161
BH	SGR	TA	11.77	171.56	9.42	76.404

Density estimates ($\hat{D}$) of black-backed jackal (BBJ) and brown hyaena (BH) within Shamwari Private Game Reserve (SGR) and a mixed used agricultural area (MUA). Snapshot method refers to the method used to calculate snapshot intervals (TA = Trigger Adjusted Effort or RDI = Recovery Driven Interval) subsequently incorporated into effort calculations (See Section 2.4.2). Site Specific *t* refers to snapshot intervals calculated using mean burst time of each specific sampling occasion. Setting Mean t refers to snapshot intervals calculated from mean burst time of all camera traps programmed with the same programmed settings (e.g. number of images in a burst, trigger intervals). *cv* = percentage coefficient of variation based on 1000 bootstrap repetitions.