Ecology of black-backed jackal (*Canis mesomelas*) in a small urban estate

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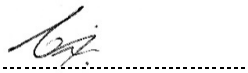
DECLARATION

I hereby declare that this thesis is my own unassisted work, and that acknowledgement has been given to the references used and assistance received. It is being submitted for the Degree of Master of Science in the Faculty of Science at the University of the Witwatersrand. It has not been submitted for any degree or examination at any other University.



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ETHICS

I received ethics clearance (2019/08/45/B) from the Animal Screening and Ethics Committee of the University of the Witwatersrand for the use of the camera traps. I also received ethics clearance (H19/09/53) from the Human Research Ethics Committee of the University of the Witwatersrand for the use of the online survey.

Contents

ABSTRACT

Most studies of black-backed jackals (*Canis mesomelas*) have taken place in areas of two extremes, where they are 1) not persecuted by people, such as in national parks, or 2) heavily persecuted, such as rural areas surrounding livestock farms. In both areas, the black-backed jackals are typically wary of people. My study was conducted in the winter of 2019 and summer of 2019/2020, involving black-backed jackals at a small urban estate, the Jackal Creek Golf Estate in the north of Johannesburg, South Africa. This area presents a unique situation where black-backed jackals are thriving and have a reduced wariness of people, which provided an opportunity to assess whether and how the black-backed jackals have adapted to living in human-altered (urban) habitats, the fastest growing land use globally. I studied the biology of the black-backed jackals in urban areas by first considering the extent to which they occur in the urban areas of Greater Johannesburg. I then conducted a specific study on the black-backed jackals occurring at the Jackal Creek Golf Estate to ascertain their activity patterns, their behaviour temporally and spatially, and their diet. I studied the species distribution through surveys of the public using online platforms and found that black-backed jackals occurred mostly in the northern parts of Johannesburg. However, the number of respondents was not large enough to draw meaningful conclusions. My study at the Jackal Creek Golf Estate was conducted mostly using camera traps to capture footage of the seasonal and daily activity profiles of the jackals and their behaviour during their active periods. I also studied the diet of the black-backed jackals through analyses of scat, opportunistically collected at the Estate in winter and summer. Activity patterns were determined using the 'densityPlot' function and 'overlap' package in R. In winter, the black-backed jackals showed a crepuscular (after 18h00) and nocturnal peak (03h00) in activity, and an extended crepuscular peak (from 19h00) and nocturnal activity (from 22h00 to 04h00) in summer in some areas of the Estate. To analyse seasonal differences in behaviour, the 'glmer' function in R was used, while temporal and spatial variation in behaviour were analysed using Pearson's chi-squared contingency table analyses. The most prominent behaviours displayed in both winter and summer were travel ($p<0.001$) and rest ($p<0.001$). In the temporal analysis of the behaviours, black-backed jackals displayed both travel and rest behaviours predominantly between 00h00 and 06h00 and again between 18h00 and 24h00, with both behaviours occurring more often in these time brackets in winter compared to summer. Spatially, all behaviours occurred in the western parts of the Estate and travel and rest were the predominant behaviours recorded in all areas of the Estate. Simpson's diversity

and Levin's standardised indices were calculated to determine diet breadth. The black-backed jackal's diet showed wide diversity, indicating a generalist diet with a large plant component (presumably incidentally consumed) (77.6%) and animal remains (67.8%). Anthropogenic matter (e.g. pieces of serviettes, glass, and fabric) occurred in the scat in almost equal percentages in both winter (46.5%) and summer (44.4%). Despite the low reported occurrence of black-backed jackals in Greater Johannesburg, the jackals at Jackal Creek Golf Estate have modified some of their behaviour and diet for urban life. Although their crepuscular peak in activity resembles that of naturally occurring black-backed jackals, the nocturnal peak suggests a change in behaviour to avoid human contact. Given their proximity to humans at the Estate, the anthropogenic content of the diet is expected, but their diet also consisted of typically naturally occurring prey, such as rodents. It would appear that black-backed jackals are urban adapters, defined as species that are able to adapt to urban areas while still making use of natural resources.

INTRODUCTION

Urban wildlife

An urban area is defined as a place of human residence, activity and associated land use developed for those purposes, usually defined by a threshold human density of about 250 000 people (Gehrt, 2010; Bateman and Fleming, 2012). As a result of increased urbanisation and a loss of favourable natural habitats globally, many wildlife species have exploited urban areas. A question that needs to be answered is whether or not wildlife has moved into or become trapped in urban environments (Gehrt *et al*., 2009). Several animals, especially mesocarnivores (i.e. medium-sized carnivores which have a more varied diet than larger carnivores), have exploited human-altered (urban) areas, such as raccoons (*Procyon lotor*), living in abundance in the Ned Brown Forest Preserve in Cook County, Illinois (Prange et al., 2003); coyotes (*Canis latrans*) in the Denver Metropolitan area of Colorado (Poessel et al., 2013); dingoes (*Canis lupus dingo*) in the Pine Rivers Shire and Maroochy Shire in southeast Queensland (Allen et al., 2013), and stone martens (*Martes foina*) that den in buildings in the towns of Bettembourg and Dudelange in Luxembourg (Herr et al., 2010). Some urban carnivores have even diverged genetically from naturally occurring relatives. For example, coyotes in southern California show greater genetic diversity in more natural areas of the State, whereas those residing in more urban parts of the State showed a decrease in genetic diversity (Adducci et al., 2020).

The challenges experienced by mesocarnivores include but are not limited to persecution by people, habitat fragmentation, limited vegetation cover, and a profusion of roads, leading to roadkill (Bateman and Fleming, 2012). However, with these challenges may also come a degree of benefits, such as the availability of anthropogenic food, which may be a key factor in achieving greater population densities and enabling a species to persist in an urban environment (Theimer *et al*., 2015). In urban environments, animals often display increased reproductive output, higher survival rates of adults and a greater affiliation to breeding sites, all of which enable these animals to reach high densities (Sol *et al*., 2013). For example, several studies report high survival rates of coyotes in urban environments (reviewed in Gehrt, 2007). Other examples include raccoons reaching densities of 41-333 individuals/km^2 in urban and suburban areas (Prange et al., 2003) compared with 0.9-55.6 individuals/km^2 in rural areas (Smith and Engeman, 2002). In rural woodland areas of Ireland, badger (M*eles meles*) population densities are 4.9 individuals/km^2 (Palphramand et

al., 2007), whereas, in the city of Brighton in the UK, population densities reached 33 individuals/km^2 (Davison et al., 2009). Spotted hyena (*Crocuta crocuta*) densities in the Wukro district of Ethiopia have been estimated at 0.52 individuals/km^2 compared with 0.33 individuals/km^2 in Hluhluwe-iMfolozi Park in South Africa and 0.02 hyenas/km^2 in Etosha National Park in Namibia (Yirga et al., 2013). All these examples show the greater population densities of species in urban environments. The proficiency with which a species can adapt to new or modified environments is vital to its success within that environment (Sih *et al*., 2011).

Species can be grouped according to their level of dependence on anthropogenic-subsidised resources (McKinney, 2002): 'urban avoiders' which deliberately circumvent urban areas (e.g. weasels (*Mustela* spp.) (Lopucki et al., 2019)); 'urban exploiters' which purposefully occupy and utilise urban environments and any associated anthropogenic foods (e.g. red foxes (*Vulpes vulpes*), coyotes (Bateman and Fleming, 2012) and hooded crows (*Corvus corone*) (Kark et al., 2007)); and 'urban adapters' which often find themselves in urban environments as a result of becoming trapped in the urban sprawl (e.g. common blackbirds (*Turdus merula*) (Kark et al., 2007) and stone martens (Herr et al., 2009)), can adapt to urban areas while still predominantly making use of natural resources (Bateman and Fleming, 2012). Urban exploiters and adapters can attain greater population densities, maintain smaller home ranges and display reduced territoriality when residing in an urban environment (Herr *et al*., 2009).

Successful urban living can be as a result of a certain level of dependence of urban wildlife on available anthropogenic resources. Successful urban carnivores are diet generalists, making use of a variety of food sources (Chace and Walsh, 2006; Sih, 2013). For example, red foxes in Zurich, Switzerland, raccoons in Ohio, USA and striped skunks (*Mephitis mephitis*) in various urban habitats of North America, which consume a broad range of food types including anthropogenic foods (Bateman and Fleming, 2012).

Despite some human residents accepting wildlife into urban spaces, some of these animals may pose potential problems (Herr *et al*., 2010), resulting in human-wildlife conflict. For example, stone martens dwell in roof spaces of buildings in the city of Luxembourg and cause property damage, staining from faeces and urine (as well as the associated odours), and noise problems (Herr *et al*., 2010). Human-wildlife conflict is defined as the state that occurs when the behaviour of a non-pest, free-living animal species begins to pose a direct and repeated threat to the livelihood or safety of a person or a community and, as a result, the species is persecuted in retaliation (Inskip and Zimmermann, 2009). These conflicts are

becoming more prevalent as a result of an increasing human population and consequent urban expansion (Graham *et al*., 2005).

Wildlife residing in urban environments may experience greater exposure to human activities which can result in habituation (i.e. a reduction in behavioural response as a result of exposure to a repeated stimulus without any sensory change; Rankin et al., 2009) to humans and human activities. Therefore, when exposed to non-threatening stimuli, it is expected that animals habituate to those stimuli (Coleman *et al*., 2008). For example, Bruintjes and Radford (2013) showed that animals habituate to loud noises if these are presented continuously for a long period. This habituation can lead to further human-wildlife conflicts and increased aggression of wildlife towards humans due to the proximity of wildlife to humans in urban areas and the lack of fear seen in animals for people (George and Crooks, 2006). Such conflicts include attacks by urban Australian magpies (*Gymnorhina tibicen*) on humans that they perceive as threats (Warne and Jones, 2003). In the Cape Peninsula of South Africa, human-wildlife conflict occurs between chacma baboons (*Papio ursinus*) and humans, where baboons are known to raid houses for food and even take food directly from people causing property damage and often retaliatory actions by people to the baboons (Kaplan et al., 2011).

Phenotypic plasticity

Assessing the biological traits that are deemed necessary for a species to be successful in urban environments is important for predicting future global trends in biodiversity (Maklakov *et al*., 2011). What will enable a species to be successful and thrive in an urban environment? One adaptation could be the phenotypic plasticity of a species (Sol *et al*., 2013). Phenotypic plasticity is defined as a single genotype being able to produce multiple phenotypes because of changes in prevailing or predicted environmental conditions (Ghalambor *et al*., 2010), and includes behavioural, morphological and physiological plasticity. Behavioural plasticity is the reaction of organisms, such as basic reflexes or pre-set action patterns, as a result of a stimulus in their environment, and the ability to adaptively modify behaviour as a function of experience (Cardoso *et al*., 2015). Behavioural plasticity includes social learning and changes in adult behaviour as a result of experience during an individual's lifetime (Snell-Rood, 2013). An example of behavioural plasticity can be seen in garter snakes (*Thamnophis sirtalis*) which display different levels of latency with regard to capturing and swallowing prey depending on their diet (Burghardt and Krause, 1999). Morphological plasticity occurs when an organism is able to develop the appropriate

morphological structures to meet environmental challenges (Travis, 1994). An example of morphological plasticity is the differing lengths of the hindlimb of the *Anolis sagrei* lizard in which those that live on wider surfaces, for instance on the ground, have longer hindlimbs than those living on narrower surfaces like twigs (Losos et al., 1999). Physiological plasticity concerns changes in mechanisms (e.g. neuroendocrine modulation) of an organism in response to or in anticipation of environmental conditions (Kingsolver and Huey, 1998). For example, house sparrows (*Passer domesticus*) alter their digestive enzyme activity according to changes in their diet (Brzek et al., 2009). Physiological and behavioural plasticity are often demonstrated over a short period of time and can be reversible, whereas morphological plasticity may occur during early life and is often much less reversible (Kingsolver and Huey, 1998).

Coyotes provide a good example of phenotypic plasticity in response to urbanisation. Coyotes show plasticity in their behaviour and diet, which potentially enables them to utilise and flourish in human-altered environments (i.e. environments in which any modification by humans exists) (Gese and Bekoff, 2004). They are reported to adjust their activity times according to human presence, for example, by decreasing daytime activity in areas frequented by humans (Gehrt, 2007). Social plasticity concerning resource dispersion and dispersal costs is often recorded in urban carnivores, resulting in reduced home range sizes, altered mating systems and increased group sizes (Bateman and Fleming, 2012). Coyotes living near people have smaller home range sizes (7.3km^2 in urban areas compared with 17.5km^2 in rural areas), high survival rates (0.62 individuals in urban areas compared with 0.20 individuals in less developed areas) (Gehrt, 2007), and as a result, greater population densities (from 0.01-0.09 coyotes/km^2 in rural areas to 0.9-2.3 coyotes/km^2 in more urban areas) (Gese and Bekoff, 2004). Although they occur at higher population densities in urban areas, coyotes still maintain their monogamous reproductive behaviour (Hennessy et al., 2012). The flexible feeding habits of mesocarnivores gives them the advantage to persist in human landscapes (Grafton, 1965). The diet breadth of coyotes in urban San Diego, California, is similar to that of their rural counterparts but differs in composition (Larson et al., 2015). However, this appears to be habitat dependent, where other coyotes in urban North America display an increase in dietary breadth (Murray et al., 2015a). Their urban diet also includes garbage produced by people, farmed fruits and vegetables, as well as remnants of domestic cats (a component absent in rural coyote diets), showing their opportunistic nature and adaptability in an urban environment (Larson et al., 2015).

The ability of species to behaviourally adapt to urban environments impacts the success of a species significantly (Jung and Kalko, 2010; Sih *et al*., 2011). For example, some insectivorous bats, such as free-tailed bats (*Molossidae spp.*), take up residence in urban environments as a result of their exploitation of artificial roosting sites created by buildings and the predation on insects around artificial lighting, like streetlights (Jung and Kalko, 2010). Some animals also change activity patterns, space use and social behaviour in urban areas (Bateman and Fleming, 2012). For example, European hedgehogs (*Erinaceus europaeus*) that have modified their nocturnal foraging such that their movements occur mostly after midnight when there is a reduction in human activity (Dowding et al., 2010), a response also exhibited in urban coyotes and bobcats (*Lynx rufus*) (Tigas et al., 2002). Other studies have demonstrated marked behavioural adjustments for urban life. For example, male great tits (*Parus major*) adjust their mating song to a shorter, faster, higher frequency in urban areas when compared with their natural counterparts (Slabbekoorn and den Boer-Visser, 2006).

In order for a species to persist in an urban area, it should display a degree of tolerance to humans and the ability to learn from conspecifics (Jung and Kalko, 2010). This degree of tolerance to humans would be in the form of habituation as seen in the Collserola Natural Park in the metropolitan area of Barcelona where wild boars (*Sus scrofa*) have become habituated to their urban environment and the humans within it as a result of being fed, directly and indirectly, by humans. This habituation of wild boars to humans has resulted in an increase in the wild boar population (Cahill et al., 2012). Another example is the habituation of grey currawongs (*Strepera versicolor*) and Carnaby's cockatoo (*Calyptorhynchus latirostris*) in Australia both of which display a reduced flight-initiation distance in urban areas compared with their rural counterparts (Metcalf et al., 2000). It has been suggested that behavioural plasticity is often the result of social learning (Reader and Laland, 2002), particularly where generations overlap and learnt information can be passed on between group members (Sih *et al*., 2011). Therefore, social learning might also contribute to the success of urban species. For example, brown rats (*Rattus norvegicus*) are more inclined to select novel foods that have been scent-marked by other brown rats, over novel foods that have not been scent-marked (Heyes, 1994). Common starlings (*Sturnus vulgaris*) follow cues from conspecifics with regard to foraging success by assessing whether conspecifics remain at or leave a foraging site as a result of the ease of foraging at the site (Galef Jr and Laland, 2005).

Resource selection/availability

Normally, animal occurrence, movement and space use are affected by predation risk, food distribution and social interactions (Gallagher *et al*., 2017). In novel or altered environments, the key factors that influence a species prevalence are the choice of available resources (e.g. food), a lack of natural enemies and the physical environment (e.g. denning areas) (Bateman and Fleming, 2012). In urban areas, food resources are often more abundant and reliable. These include human refuse, synanthropic rodents and birds, pets, or food deliberately left out by people for free-living animals, which may unintentionally lure wildlife into urban areas, including mesocarnivores (Bateman and Fleming, 2012). In addition, the availability and distribution of food are often heterogenous as a result of clustered and abundant anthropogenic food resources, which can then affect the spatial distribution and movement of some mammals (Prange *et al*., 2004).

Easily accessible and/or high energy food (e.g. carbohydrates) reduces foraging costs, leading to rapid population growth (Prugh *et al*., 2009; Theimer *et al*., 2015). In addition, animals use habitats and exhibit movement patterns that will increase energy acquisition and optimise their fitness (Gallagher et al., 2017). When animals display efficient use or sharing of resources, it allows them to succeed at higher densities (Sol *et al*., 2013). This sharing could happen on many levels, such as temporal or spatial sharing of resources, such that individuals can still maintain their energetic requirements in smaller areas, which urban environments often present (Schoener, 1974; Sol et al., 2013). This is demonstrated in the two mongoose species occurring in an urban estate in South Africa, where the slender mongoose (*Galerella sanguinea*) and yellow mongoose (*Cynictis penicillata*) have modified their timing of consumption of similar diet components so as to not overlap temporally and allowing them to co-exist in the estate (Cronk and Pillay, 2019).

Urban areas also offer safety, in the form of low predation pressure (Gering and Blair, 1999) as a result of a reduced number of natural predators (Valcarcel and Fernandez-Juricic, 2009; Fischer et al., 2012). Consistency with regard to seasonal human behaviour towards animals and a lack of natural predators in urban areas can result in a change in anti-predator behaviour of urban wildlife (Uchida et al., 2016). Such changes are often observed as a decrease in flight initiation distance, as seen in the Cape ground squirrel (*Xerus inauris*) in the Johannesburg Zoo, South Africa (Chapman et al., 2012). A decrease in flight initiation distance as a result of a decrease in natural predators has also been recorded in Eurasian red squirrels (*Sciurus vulgaris*) in the Tokachi region of central Hokkaido, Japan (Uchida et al.,

2016), and in a variety of urban birds in Ile-de-France and Bretagne, France and Northern Jutland, Denmark (Moller, 2008).

Species may also select to reside in novel or altered environments as a result of the alternative available den sites, allowing them to occur in closer proximity to humans and to exploit the associated advantages (Majumder et al., 2016). An abundance of anthropogenic structures and natural vegetation found in gardens and parks in urban areas can be utilised by animals for denning, offering animals refuge within these novel environments (Bateman and Fleming, 2012). Some examples include stone martens which show a penchant for denning in inhabited buildings in towns in Luxembourg due to the warmth and insulation offered (Herr et al., 2010). Similarly, Virginia opossums (*Didelphis virginiana*) in California demonstrate a preference for nesting inside or beneath buildings in urban areas due to the shelter of these structures (Maestrelli, 1990).

In urban carnivores, increased population density can occur as a result of greater resource (e.g. food and shelter) availability (Bateman and Fleming, 2012). High densities of animals can also occur in urban environments as a result of a lack of other competitive species (i.e. interspecific competition) (Lang and Benbow, 2013), and as a result of reduced dispersal of individuals (Babinska-Werka *et al*., 1981). However, increased density can result in some degree of intraspecific competition (Hiscocks and Perrin, 1987) because of similar ecological and energetic requirements (Gilad, 2008; Kimley *et al*., 1996).

When intraspecific competition leads to resources becoming limited, optimal foraging theory predicts that individuals will broaden their diet and become more opportunistic (Araujo *et al*., 2008). This is seen in urban coyotes in North America which show an increased dietary breadth in comparison to rural coyotes as a result of the addition of anthropogenic foods to their diet (Murray et al., 2015a). Urban-dwelling blue tits (*Cyanistes caeruleus*) in Glasgow, Scotland, feed their nestlings a broader diet than that fed to nestlings in forest sites because of the difference in food availability (Pollock et al., 2017).

Natural areas abutting urban areas

Habitat interfaces, where natural areas meet urban areas, can be beneficial for many wildlife species (Soule, 2008). In order to preserve species and biodiversity in urban areas, space planning needs to incorporate corridors that link natural habitats found within or between urban areas, which may be important for species that need a variety of habitats for their survival, particularly those that are highly mobile (Soule, 2008; Gallo et al., 2017).

These corridors are important in maintaining continuity between natural habitats for animals, alleviating some of the negative effects of fragmentation for urban species (Forman and Godron, 1981). With some areas of South Africa still being underdeveloped, these corridors may still exist geographically as untouched natural habitats abutting urban areas.

Urban green spaces provide many important environmental services for various species (Gallo et al., 2017). Examples include urban green spaces functioning as replacement habitats, such as the use of golf courses by various avian communities in New Mexico in place of their natural riparian habitats (Merola-Zwartjes and DeLong, 2005), refuge habitats for species such as bumblebees (*Bombus* spp.) in the urban parks of San Francisco (McFrederick and LeBuhn, 2005), and for use as dispersal or movement corridors as seen in several small bird and mammal species (Bolger et al., 2001). Mammals, being more susceptible to the physical barriers formed by roads, buildings, and increased human activity in urban areas, may frequent urban green spaces, corridors and natural habitats abutting urban areas to interact with conspecifics (e.g. for mating) (Gallo et al., 2017).

Connection of natural areas through corridors may result in greater population density within urban areas (Bolger et al., 2001), as seen in white-footed mice (*Peromyscus leucopus*) in fragmented habitats that are connected (Fahrig and Merriam, 1985), and in three butterfly species (*Junonia coenia, Euptoieta claudia,* and *Phoebis sennae*) in habitat patches connected by corridors than in habitat patches which are isolated (Haddad and Baum, 1999). Some of these corridors may function as habitat linkages, providing the necessary resources for reproduction and survival, whereas others may function merely as movement corridors between natural areas without supporting any resident individuals (Bolger et al., 2001).

Study species

The black-backed jackal (*Canis mesomelas*) is a member of the family Canidae and is one of nine species of the genus *Canis*. It is endemic to sub-Saharan Africa and southern Africa (Figure 1) (Estes, 1992; Wilson and Reeder, 2005; Minnie *et al.*, 2016), with a finer scale regional distribution available for South Africa from 2016 (Figure 2). In South Africa, it is found throughout the country, generally showing a preference for areas with scattered bush (Estes, 1992), but thus far have appeared to be absent in more urbanised areas. However, with its generalist diet and flexible behaviour, it is expected that they may become accomplished urban exploiters (Nattrass *et al.*, 2017). The habitats used by black-backed jackals are varied and often based on seasonal changes in prey abundance; they utilise more closed habitats,

such as areas with denser vegetation, in winter as a result of the retreat of prey into those areas (McKenzie, 1993).

Figure 1. Distribution map of Black-backed jackal in Africa, showing a disjunct distribution in southern and north-eastern Africa (adapted from Hoffmann, 2008).

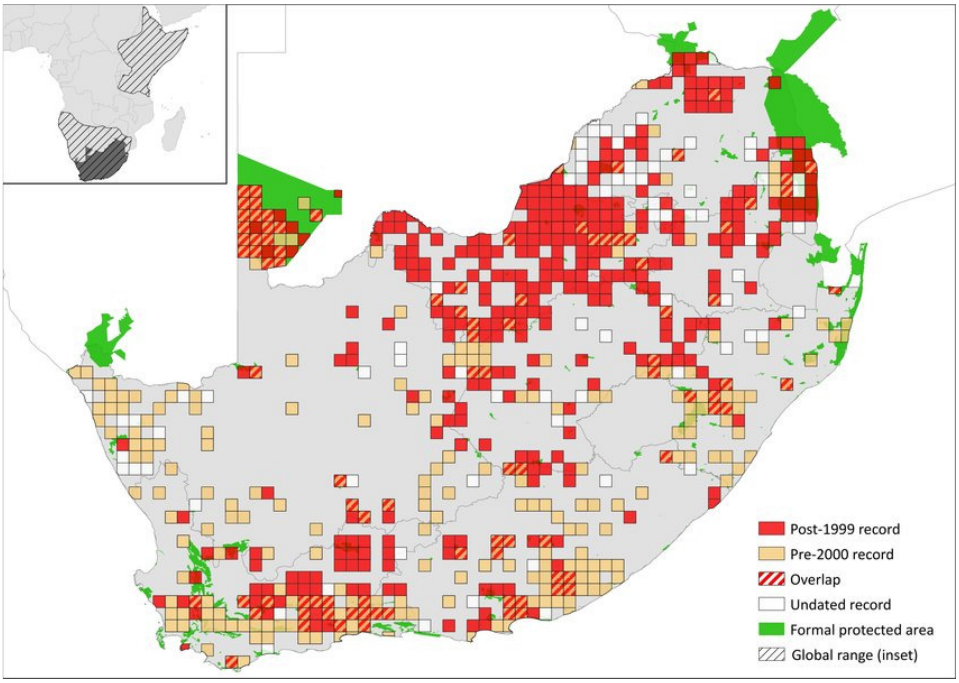


Figure 2. Distribution map of Black-backed jackal in South Africa (from Minnie et al., 2016).

Black-backed jackals are identified by a reddish-brown to tan coloured coat with a distinctive black saddle flecked with silvery-white hair, black-tipped tails, and white throats and underparts (Estes, 1992). They stand between 38-48 cm tall, with males weighing

between 6.8-9.5 kg and females are between 5.4-10 kg (Estes, 1992). Other than a slight difference in size, there is little to no sexual dimorphism (Carnaby, 2007).

Black-backed jackal activity is bimodal, with peaks in activity occurring in the early mornings and evenings (Ferguson *et al*., 1988; McKenzie, 1993). They are omnivorous, with a diet consisting of insects, rodents and birds, carrion, hoofed domestic livestock, hares and antelope, and vegetable matter, and so are considered to be mesocarnivores (Grafton, 1965; Rowe-Rowe, 1983; Hiscocks and Perrin, 1987). They are both predators and scavengers, altering their diet based on food availability (Rowe-Rowe, 1983; Jenner *et al*., 2011; Nattrass *et al*., 2017). This opportunistic, generalist diet may contribute to their success in human-altered environments (Nattrass *et al*., 2017).

Black-backed jackals often occur as monogamous pairs that actively maintain and defend territories against conspecifics. Black-backed jackal also display site fidelity with regard to territories, in which they re-use dens each year for raising litters (Jenner et al., 2011). Both male and female black-backed jackal actively participate in scent-marking and territory defence (Rowe-Rowe, 1982; Estes, 1992; Carnaby, 2007), and both parents also rear the young (Estes, 1992). Mating begins in June and continues into July (McKenzie, 1993), resulting in 3-4 (up to 6) pups (Estes, 1992) between August and November after a 60 day gestation period (Estes, 1992; McKenzie, 1993). Black-backed jackals are facultatively co-operative breeders: subordinates often remain with the breeding pair until the next season and assist with the rearing of the next generation of pups (Estes, 1992; McKenzie, 1993; Nattrass *et al*., 2017). Weaning occurs between November and January (Kaunda and Skinner, 2003). The offspring disperse from the natal den between February and April (Kaunda and Skinner, 2003) when they are between 8-12 months of age (Estes, 1992; McKenzie, 1993). Subordinates reach sexual maturity after 11 months; some will disperse from the natal den at this stage, whereas others will delay their own reproduction and remain behind as helpers for an additional year (Estes, 1992; McKenzie, 1993; Nattrass *et al*., 2017).

Home range sizes of black-backed jackals are highly variable and have been recorded to be between 7.1-91.5 km^2 (Hiscocks and Perrin, 1988; Nattrass et al., 2017) and occur at densities of 0.37 jackals/km^2 in Pilanesberg National Park, South Africa (Yarnell et al., 2013) to 9.8 jackals/km^2 in Cape Cross Seal Reserve, Namibia (Jenner et al., 2011). Environmental conditions, such as food resources, appear to impact the size and use of home ranges, as well as densities of black-backed jackals (Kaunda, 2000; Jenner et al., 2011; Nattrass et al., 2017). Breeding pairs are territorial and there is no home range overlap with other mated pairs (Rowe-Rowe, 1982). However, home ranges of subordinates often overlap with, and are

larger than, those of mated pairs (Rowe-Rowe, 1982). At times, home range overlap may occur in adults when there is a profusion of food resources, as seen at the Cape Cross Seal Reserve in Namibia, where a high level of home range overlap occurs in conjunction with a year-round, abundant food source of predominantly seals (Hiscocks and Perrin, 1988). Black-backed jackals are opportunistic co-operative hunters when necessary (Nattrass *et al*., 2017), as observed in Etosha National Park in Namibia where a group of six individuals successfully killed a springbok (*Antidorcas marsupialis*) as a collaborative effort (Krofel, 2007).

Context of the study

Most studies of black-backed jackals (*Canis mesomelas*) have taken place in areas of two extremes, where they are 1) not persecuted by people, such as in national parks (Ferguson, 1978), or 2) heavily persecuted, such as rural areas surrounding livestock farms (du P Bothma, 1971). In both areas, the black-backed jackals are typically wary of people. My study involved black-backed jackals at a small urban estate, the Jackal Creek Golf Estate, an area that presents a unique situation where black-backed jackals are thriving and have a reduced wariness of people.

A pilot study established that a relatively large, breeding population (approximately 16 individuals) of black-backed jackals occurs in and utilises the Jackal Creek Golf Estate (hereafter Estate, as appropriate), north of Johannesburg, South Africa (Weil, 2017). At the time of my study, there were three breeding pairs of black-backed jackals at the Estate, each with four pups. There were also two lone jackals presumed to be from previous litters, attempting to disperse. This equates to approximately 20 black-backed jackals at the Estate in winter 2019. Each year, each breeding pair produces a litter size of approximately 4-5 pups per litter, with one pair producing two litters a year. This results in a fluctuation of the population on an annual basis of between 20-24 jackals, giving a population density of 12.05-14.46 jackal/km^2.

Whether these animals have become trapped within this urban environment or have moved into it because of available opportunities is unknown. What is also unknown is their diet at the Estate, their use of breeding areas, intraspecific competition, and ultimately whether and how their behaviour has changed (e.g. diet, activity patterns and behaviour) compared to naturally occurring conspecifics.

AIMS, OBJECTIVES AND PREDICTIONS/QUESTIONS

My study had two aims. The first aim was to establish the occurrence of black-backed jackals in Greater Johannesburg, to ascertain the prevalence of the species in urban Johannesburg. The second aim was to assess the mechanisms that allow black-backed jackals to live in urban areas, by focussing on the population occurring at Jackal Creek Golf Estate. I had four objectives.

Objective 1. To establish the current black-backed jackal areas of occurrence and absence in Greater Johannesburg, using sightings reported by members of the public via social media.

- *Prediction.*

  With a rapid increase in urbanisation in the Greater Johannesburg region, natural habitats for the black-backed jackals (see Figure 2) are likely to have diminished, resulting in the possible movement into, or isolation of, these animals in urban environments. I expected the black-backed jackals to be more prevalent in some areas of Johannesburg than others, occurring close to natural (less urbanised) areas.

Objective 2. To examine the activity patterns of the black-backed jackals within the Estate, particularly the general daily activity profile and seasonal variation in activity.

- *Predictions*
  - A pilot study by Weil (2017) suggested that the black-backed jackals are most active in the early mornings and at night, representative of a typical bimodal peak in activity as seen in black-backed jackals in their natural environment (McKenzie, 1993). I predicted to find the same bimodal peak in activity.
  - Black-backed jackals living in natural environments tend to show a decrease in their number of hours of activity during summer as a result of an increase in resource availability (Kaunda, 2000). I predicted that there would be little to no variation in seasonal activity of the jackal at the Estate because of the predictability of the environment and the apparent year-round availability of resources (e.g. anthropogenic foods).

Objective 3. To assess the temporal and spatial patterns of behaviour of the black-backed jackals within the Estate.

- *Predictions*
  - I predicted that the jackals would show temporal variation in behaviours, displaying behaviours like resting during the day and foraging more at night. Diurnally, naturally-occurring black-backed jackals display predominantly flight behaviour and resting, whereas, nocturnally, display predominantly hunting/foraging behaviour and locomotion (Kaunda, 2000).
  - I predicted that the black-backed jackals would use specific areas of the Estate for different behaviours, for example between areas near denning sites (where resting is more likely) compared with communal areas (areas between den sites) where foraging and travel are likely to occur. Nattrass et al. (2017) found that black-backed jackals change their behaviour spatially as a consequence of local environmental conditions, such as food availability, human persecution, and the presence or absence of competitive species.

Objective 4. To establish the diet of the black-backed jackal population at the Estate through scat analysis.

- *Predictions*
  - Free-living black-backed jackals have a wide diet breadth based on the availability of resources within their habitat (Minnie *et al*., 2016). I predicted that the diet of the black-backed jackals at the Estate would be wider than that of populations living in natural environments. The diet would also consist largely of the fauna and flora found at the Estate, such as birds, rodents, insects, and vegetation.
  - I predicted that anthropogenic food would be among the main components of the black-backed jackals' diet at the Estate, despite human residents at the Estate being urged not to feed the black-backed jackals.

MATERIALS AND METHODS

Species distribution in Greater Johannesburg

To establish the occurrence of black-backed jackal in the Greater Johannesburg area, I surveyed the public using social media and a Google form. A Facebook page was created in which members of the public could join and share and access the link to a Google form (Appendix 1) to report black-backed jackal sightings. I distributed the Facebook page through friends and family, and as many online platforms as possible, such as conservation websites (e.g. Modderfontein Conservation Society website) and community pages (e.g. Greenstone Hill Community). The Google form was created using Google drive and enabled people to report black-backed jackal sightings in the questionnaire. The questionnaire included the following questions, whether the public had seen black-backed jackals within a 30 km radius from the Johannesburg CBD (Figure 3), how many they had seen, whether there were pups (to indicate breeding), and a location (GPS co-ordinates or a physical address) of the sighting. I recorded the sightings and mapped them to show the reported distribution within the Greater Johannesburg area.

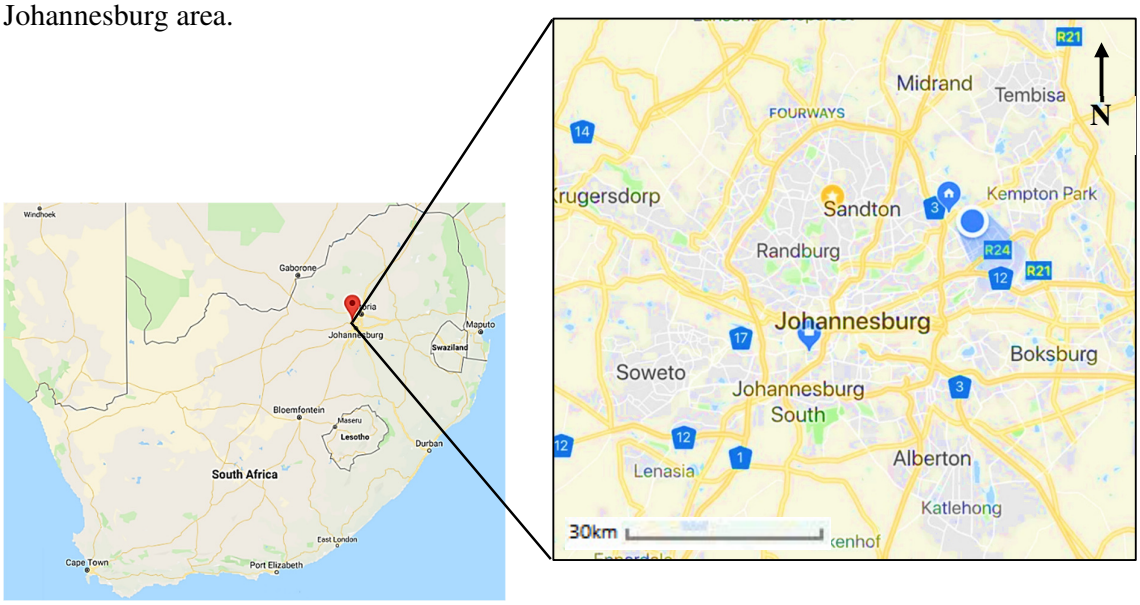


Figure 3. The Greater Johannesburg area in South Africa (inset) that was sampled to establish black-backed jackal occurrence.

The Jackal Creek Golf Estate population

The field work for this study took place within Jackal Creek Golf Estate (26.0589°S, 27.9220°E), located in northern Johannesburg, South Africa (Figure 4). This approximately 166 ha estate consists of an 18-hole golf course, including a club house and other sports facilities, and a residential area, covering approximately 45% of the Estate. There was ongoing housing development at the Estate during my study. There was a stream running through the Estate with numerous small dams and patches of both indigenous (e.g. wild olive (*Olea europaea africana*) and mountain karee (*Searsia leptodictya*)) and alien (e.g. eastern cottonwood trees (*Populus deltoides*) and west Indian lantana (*Lantana camara*)) vegetation throughout (per obs.). The boundary of the Estate consisted of brick walls as well as palisade fencing, potentially limiting the movement of black-backed jackals beyond the Estate boundaries, but not preventing it. Numerous bird and reptile species were found at the Estate which could be potential food sources for the black-backed jackals. Examples include helmeted guineafowls (*Numida meleagris*), hadeda ibis (*Bostrychia hagedash*), spotted thick-knees (*Burhinus capensis*), feral pigeons (*Columba livia*), Nile monitors (*Varanus niloticus*) and Rock monitors (*Varanus albigularis*), as well as many other birds commonly found in urban areas and golf courses in Johannesburg. Human residents at the Estate have domestic dogs and cats which, if the opportunity presented itself, might have been at risk of predation by the black-backed jackals. Some of the residences were fenced, limiting access of the black-backed jackals to these gardens, whereas others were unfenced. Rodents frequently connected with human presence and urban areas, such as rats *Rattus sp.* and house mice (*Mus musculus*) might also have constituted part of the black-backed jackals' diet. They could have also supplemented their diet with anthropogenic foods supplied either directly by residents or through scavenging on human garbage.

Figure 4. An aerial image of Jackal Creek Golf Estate in the north of Johannesburg and its location in South Africa (inset). The outline of the Estate is shown in dark blue. The green spaces are the golf course and other open spaces. Housing is shown in the small regular units.

Camera trap footage

Activity patterns

Camera traps are a useful method of data collection since they minimize environmental disturbance and allow for non-invasive observations of animals (Rovero *et al*., 2014). Five camera traps (Bushnell's Essential trophy cameras with infra-red activation and motion sensors, Bushnell Corporation, Overland Park, Kansas) were rotated to various sites across the Estate and used to assess the space use and daily activity of the jackals (Figure 5). In winter, cameras were placed at a total of 33 sites for 92 days compared with a total of 36 sites for 91 days in summer. The presence and behaviour of jackals were captured onto 16GB memory cards. Cameras were left at the same site for two weeks at a time, after which they were moved to a new location (a change in the camera direction was also considered as a new location/site; see later), batteries replaced and footage from memory cards was downloaded. The camera traps were set at varying heights above the ground, ranging from ground level to 1.5 m above ground, according to location and the field of view offered (i.e. to provide an unobstructed field of view). The cameras were set to capture video footage of 30 s after a 5 s delay period between triggering of the camera. Some cameras were set to low sensitivity to

avoid repeated capturing of any grass and plant movement. All cameras operated with these settings 24 hours a day.

The locations of the camera traps were initially based on observations of areas of high black-backed jackal frequency and the results of the pilot study (Weil, 2017). At times, the cameras were not moved to a new location but rotated to face another direction at the same site based on the previous two weeks footage. This rotation was considered when footage showed jackals moving out of the view of the camera in the first two weeks, so the cameras were rotated to achieve an almost 360° view of these particular locations. New locations were chosen to cover as much of the study area (Estate) as possible, according to the availability of suitable mounting posts to attach the cameras and were limited to non-residential areas in order to respect the privacy of residents.

The Estate was divided into eight cardinal zones to enable data interpretation, as described below. There was not an even number of cameras per cardinal zone, per season (Figure 5).

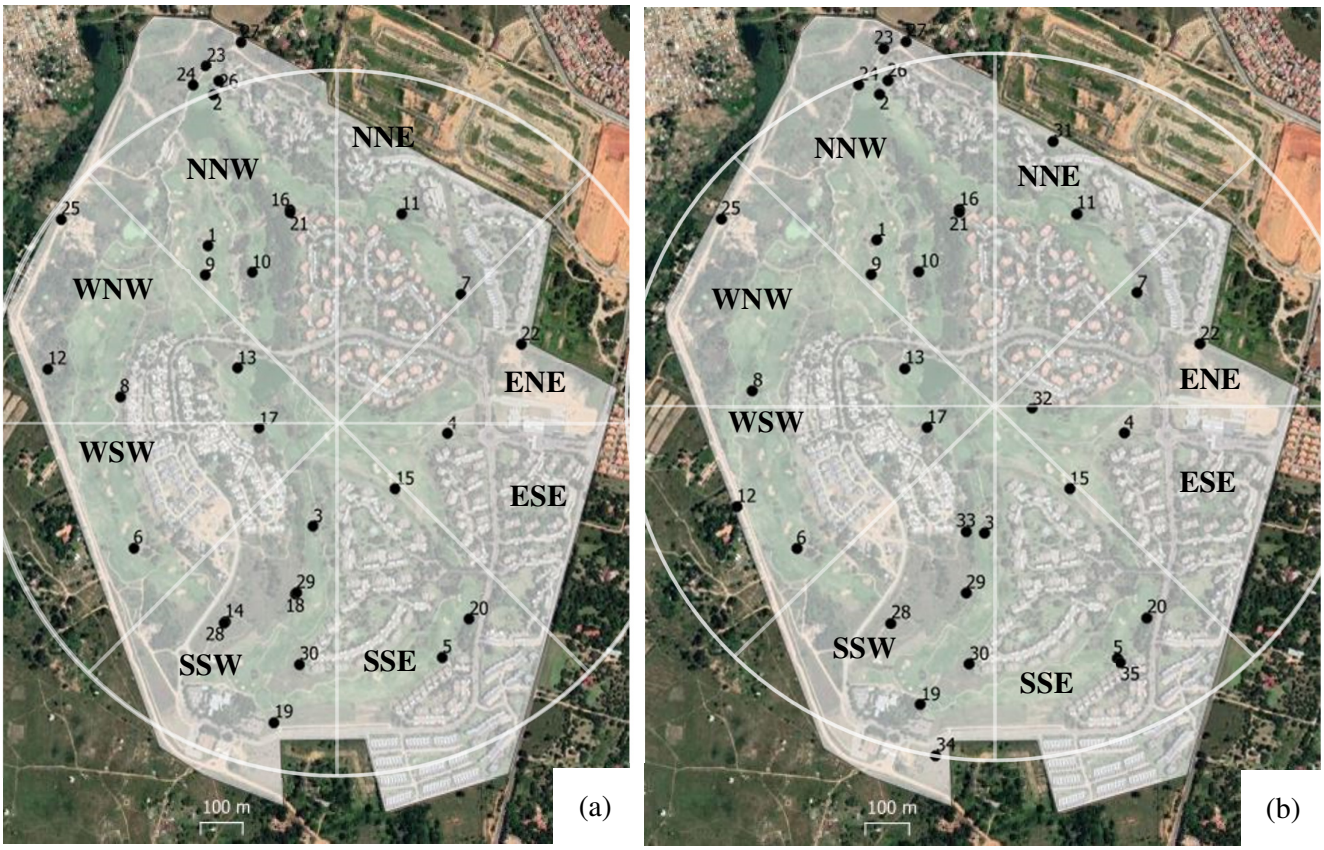


Figure 5. Camera trap placements (black dots) at Jackal Creek Estate in (a) winter (June – August 2019) and (b) summer (December 2019 – February 2020). The Estate was divided into eight cardinal zones to assess space use and behaviour.

Photographs and video footage were automatically time and date stamped. From the footage containing black-backed jackals, the following was recorded: GPS location of the camera, date, time, number of black-backed jackals, and behaviour of the jackals. Since individuals could not be identified from the videos, the maximum number of black-backed jackals occurring in footage captured within a half-hour time frame was recorded to avoid over-sampling (Norris *et al*., 2010; Jenks *et al*., 2011).

From the video footage, an assessment of daily and seasonal black-backed jackal activity and space use were recorded (below). The time and number of black-backed jackals captured in the footage was used to assess activity patterns. This data was also used to assess the spatio-temporal occurrence of the jackals, as well as their movement patterns within the Estate.

Behaviour

For both winter and summer, video footage of the black-backed jackals was extracted, and their behaviours were scored. I used 1/0 sampling (with 1 indicating the behaviour was displayed and 0 indicating the behaviour was not displayed) per $\pm$30 s camera trap footage for each season, to record the frequencies of the seven behavioural categories: travel, rest, forage, play, affiliative, aggression and other behaviours.

Travel was recorded when black-backed jackals moved through the cameras' field of view during the 30-second footage after the camera sensor was triggered. Rest was recorded when the jackals lay down within the field of view of the camera and remained within view during the 30-second footage. Forage included sniffing or scratching at the ground, as well as when the jackals were visibly consuming food. Play was recorded by play signals (e.g. play bow) displayed by the jackals, interactions involving non-aggressive posture and playing with objects (e.g. a shoe). Affiliative behaviour was identified when the jackals displayed allogrooming and greetings typical of canids (e.g. naso-anal sniffing). Aggression included teeth-baring displays, biting, and chasing one another. Other behaviours included any behaviours that did not fall into any of the above categories, such as vigilance (e.g. head and ears raised), calling and maternal care (e.g. regurgitation of food for pups), which occurred infrequently. The blacked-backed jackals were not marked since their capture and marking was not approved by the management of the Estate. Thus, I could not tell whether social interactions (especially aggression) took place within or between groups.

To assess differences in behaviour seasonally, the number of times each behaviour was performed was counted per camera trap site at the Estate, per season. The time at which

the various behaviours took place was divided into four time brackets, Night (00h00 to 06h00), Morning (06h00 to 12h00), Afternoon (12h00 to 18h00) and Evening/Night (18h00 to 24h00). The sum of the frequency of each behaviour for each time bracket was calculated and analysed statistically (below). This was done to generate a simple framework to assess the temporal occurrence. Using the eight cardinal zones (i.e. NNE, ENE, ESE, SSE, SSW, WSW, WNW, and NNW) (Figure 5), the sum of the frequency of each behaviour in a zone was calculated and analysed statistically (below). This was done to help generate a simple framework to assess space use by the blacked-backed jackals.

Diet

Scat analysis

Scat analysis is a simple, non-invasive field sampling method that can be used to establish the diet of carnivores (Kaunda and Skinner, 2003; Breuer, 2005; Klare et al., 2011). Black-backed jackals use faeces to mark territorial borders (Loveridge and Nel, 2004), often defecating on prominent objects like rocks or grass tufts alongside pathways and roads (Humphries *et al*., 2015). I used this, as well as the texture of the scat, to distinguish black-backed jackal scat from that of domestic dog scat; black-backed jackal scats have a coarser texture and often contain fur (pers obs.). Black-backed jackal scat can also be identified based on the shape, having a distinctive pointed end (Chame, 2003). Sampling in both seasons was done opportunistically by my walking around all areas of the Estate to locate scat samples. Only scat deemed 'collectable' and not eroded were collected for analysis (Ciucci *et al*., 1996). Once identified, I photographed the scat samples and collected them using plastic bags. I placed the samples in individual plastic bags and labelled them according to a unique sample number, GPS location, date, and estimated freshness. Freshness or age of the scat was determined by their colour, with darker scats assumed to be fresher (1-3 days old) and lighter scats older (a month plus) (Figure 6). The exact age of the scat could not be determined. I then stored the samples in a freezer at the University of the Witwatersrand until the analysis later.

Figure 6. Three colour classes of jackal scat used to age the scat collected: **(i)** darkest and most recent; **(ii)** intermediate colour; **(iii)** lightest and oldest.

I collected 43 scat samples in winter and 27 scat samples during summer. I oven-dried the samples overnight at 60°C (Kaunda and Skinner, 2003) at the research lab at the University of the Witwatersrand and weighed them thereafter to the nearest 0.1 gram. Each scat sample was soaked in boiling water for approximately five minutes until soft, and broken up using gloved hands and forceps (Rowe-Rowe, 1983; Humphries *et al*., 2015), and turned out onto a mesh sieve of 0.5 x 0.5 mm over a plastic container. From the material that remained on the sieve, I extracted all undigested remains and placed them into containers for further analysis. Thereafter, the remaining components were air-dried for at least a week and re-weighed to the nearest 0.1 gram. These components comprised predominantly of fur and unrecognisable particles.

I sorted the separated undigested materials according to their type: anthropogenic matter (plastic, wrappers, tin foil), arthropods (exoskeletons, legs and elytral remains), bird (hollow bones and feathers), dicotyledonous plants (twigs and net-veined leaves), fruits and seeds, mammal remains (bones, hair, teeth, and claws), monocotyledonous plants (grass and other parallel-veined leaves), and unidentifiable vertebrates (pieces of bone). For any materials that were difficult to identify, I consulted the various taxonomic specialists available in the School of Animal, Plant and Environmental Sciences, University of the Witwatersrand for assistance. Included in the unidentifiable vertebrates' category were any indeterminate bone fragments which could have included chicken (*Gallus gallus domesticus*) or lamb (*Ovis aries*) bones, that the black-backed jackals do not have access to naturally.

Scat analysis is an indirect method of determining the diet of an animal. To prevent any bias towards a particular food group (e.g. smaller or larger food items), it is recommended that multiple methods of analysis are employed (Klare et al., 2011). I used 3 protocols: 1) frequency of occurrence; 2) numerical frequency; and 3) percentage mass

contribution of food items to provide a quantitative metric, which is important for the assessment of smaller food items. The former two protocols provide qualitative metrics, important for assessing larger food items (Klare et al., 2011). The use of various scat analysis methods is also important for comparison with other studies of scats.

For each season, I tallied and noted the number of occurrences of each component for all the samples, and calculated the frequency of occurrence of scat components, numerical frequency, as well as percentage mass contribution for each item. The frequency of occurrence was calculated by dividing the total frequency of each category by the total number of scats analysed and recorded as a percentage. I calculated the numerical frequency by dividing the percentage occurrence of a category by the total number of occurrences of all the categories. For example, in winter, 20 out of the 43 collected samples contained mammalian remains, and 220 remains of various categories were in the 43 samples, yielding a 9.1% numerical frequency ($\frac{20}{220} \times 100 = 9.1\%$) and 46.5% frequency of occurrence ($\frac{20}{43} \times 100 = 46.5\%$) of mammalian remains in winter. Percentage mass contribution was calculated by dividing the total mass of each category by the total mass of the samples. Together, I used these calculations to determine the importance of different components in the diet of the jackals at the Estate.

Diversity indices are used as a metric assessment of diet breadth. I calculated the Simpson's diversity index, using $D = 1 - \left(\frac{\sum n(n-1)}{N(N-1)}\right)$, with D = Simpson's diversity index; n = number of occurrences of a specific food item; and N = total number of food items, of the scat components within seasons and the overall sample in order to ascertain the diversity of the black-backed jackals' diet within the Estate (Krebs, 1998). Simpson's diversity index is useful in determining diversity in a population's diet since it considers both depth and uniformity within the diet (Bibi and Ali, 2013). The index ranges between 0 and 1, with 0 showing a diet of little diversity and 1, a diet with high diversity. I also calculated the Levin's standardised index within seasons and the overall sample, using: $B_i = \frac{1}{1-n}\left(\frac{1}{\sum jp_{ij}^2} - 1\right)$, with B_i = Levin's standardized index for predator i; p_{ij} = proportion of diet of predator i that is made up of prey j; and n = number of prey categories, (Levins, 1968). This index was also based on the number of occurrences of each category in the scats. Levin's standardised index was used since it accurately indicates whether the diet is more specialised or generalist (Feinsinger et al., 1981). This index also ranges between 0 and 1, with 0 showing a specialist diet and 1, a generalist diet.

Data analysis

Data was analysed using R software (www.r-project.org, R version 1.2.1331). Data sets were checked for departure from normality using the Shapiro Wilk test and non-parametric analyses were performed since the data set was departed from normality. Statistical tests were two-tailed, and alpha was set at 0.05.

Species distribution

The data for species distribution was described due to the low number of responses to the survey.

Activity

Using the 'densityPlot' function in R, the activity pattern for jackals at each site for winter and summer was plotted based on the time and number of sightings (how often blacked-backed jackals were recorded in video footage) at the site, as well as to plot the overall winter and summer activity of the jackals. The 'overlap' package in R was then used to analyse the overlap of activity of each site in winter with the overall winter activity (a sum of the activity in all the sites in winter), and the overlap of activity of each site in summer with the overall summer activity (a sum of the activity in all the sites in summer), to assess unusual activity at particular sites. The 'overlap' was also used to assess the overlap of the overall winter and overall summer activity.

Behaviours

To analyse seasonal differences in behaviours, which were not normally distributed, I used the 'glmer' function (lme4 package) for each behaviour separately. In each model, behaviour was the dependent variable and season was the fixed factor. Time of day was nested in season because the timing of activity of the jackals varied seasonally. The camera trap placement site was a random factor because the placement and number of camera traps that captured footage varied seasonally. Behaviours occurred at low frequencies and thus, only travel and rest could be statistically compared. However, comparisons were still made between behaviours for each season for time and space.

Temporal and spatial variation in behaviour were analysed within and between seasons using Pearson's chi-squared contingency table analyses, in which time periods or cardinal zones were the independent variables. Only behaviours that were scored at least once

were considered for analysis. The contribution to the chi-squared analyses was then run to identify pairwise relationships between season and cardinal points or time periods. In these analyses, I considered the two most prominent behaviours in both seasons, i.e. travel and rest (see Results). I ran Spearman rank correlations between the number of times black-backed jackals were observed in camera trap footage in a cardinal zone and the frequency of travel and rest behaviours in order to establish whether the number of times a behaviour displayed was a function of the number of occurrences of the jackal within a cardinal zone. Regressions were determined for each of these behaviours for each season.

Scat components

Chi-squared analysis was performed for frequency of occurrence, numerical frequency, and percentage mass contribution in order to analyse whether the number of scat components differed by chance (i.e. a null model). I used pairwise chi-squared analyses of the different components to establish which components occurred more frequently per season and between seasons for the frequency of occurrence, numerical frequency, and percentage mass contribution.

RESULTS

Species distribution

Although the survey was distributed through multiple platforms, few people completed the survey. In total there were 12 respondents to the surveys, nine of whom reported having seen black-backed jackals in the Greater Johannesburg area. The number of individual jackals reported by the nine respondents is shown in Figure 7.

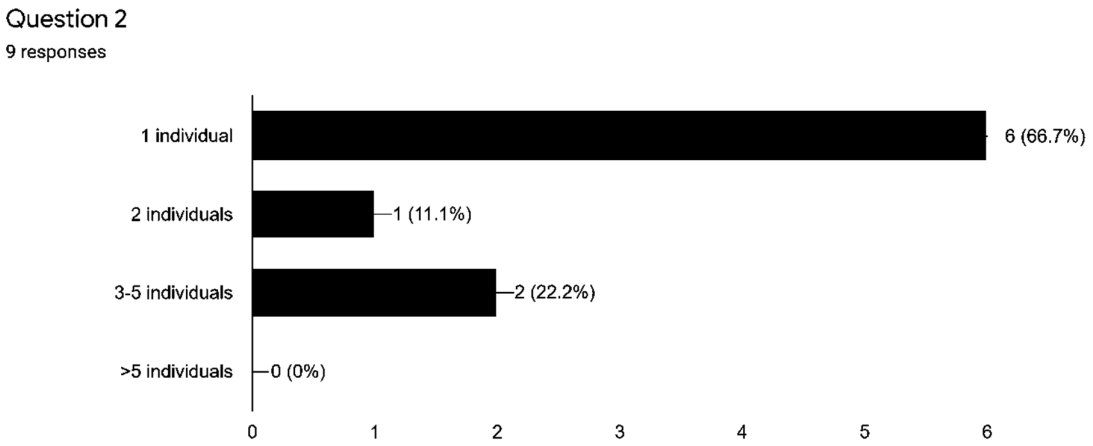


Figure 7. Results of Question 2 from the survey asking how many jackals respondents saw together in one sighting.

Question 3 asked respondents whether they had seen jackal puppies during the sightings, to which 33.3% (n=3) of respondents answered yes. The last question of the survey asked for a location of the sightings, which were plotted using Goole Maps (Figure 8). The collected data showed a general occurrence in the northern parts of Johannesburg. However, overall, the sample was not large enough to generate meaningful conclusions.

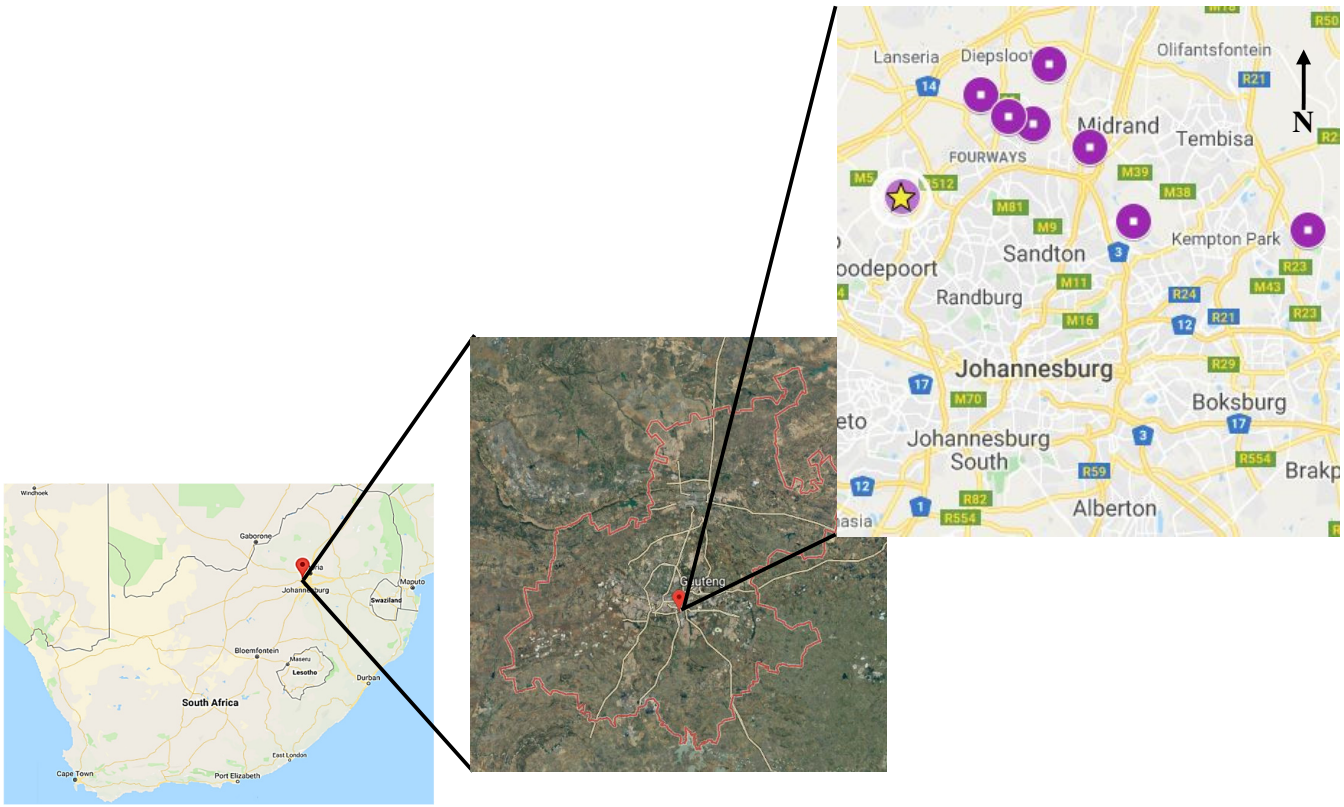


Figure 8. Plot of black-backed jackal sightings in Greater Johannesburg, reported by nine respondents in an online survey. The star = Jackal Creek Golf Estate.

Activity patterns

During winter, the overall activity (appearance on camera trap footage) of the black-backed jackals peaked at two distinct times. There was a crepuscular peak after 18h00 and a nocturnal peak just after 03h00 (Figure 9). Overall activity was low in the afternoon, between 12h00 and 16h00.

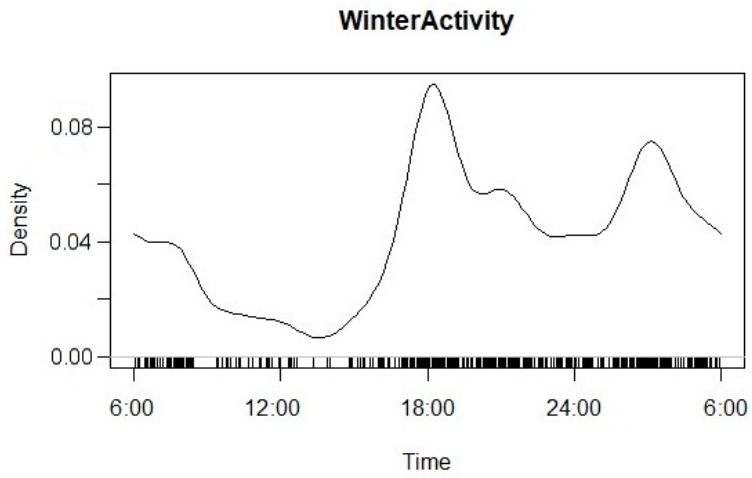
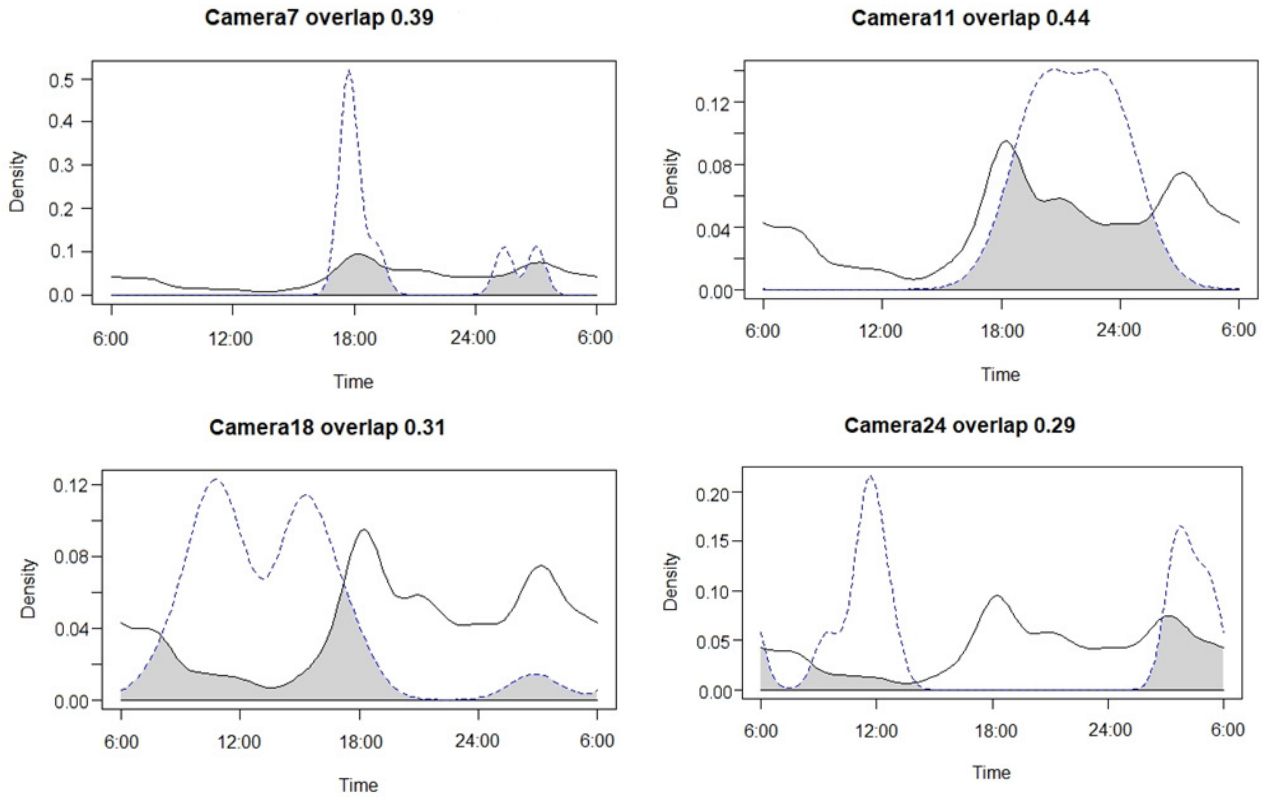


Figure 9. Overall winter activity displayed by the black-backed jackals at the Jackal Creek Golf Estate from camera-trap footage, showing a peak at dusk and during the night. The data was plotted using 'densityPlot'.

Site-specific differences in winter

Unusual activity was identified at six sites. Unusual activity was determined by an overlap coefficient of less than 0.5, indicating that the overlap of activity at a particular site coincided with less than half of the overall activity seen during the season, as occurred at sites 7, 11, 18, 24, 25 and 27 (Figure 10).



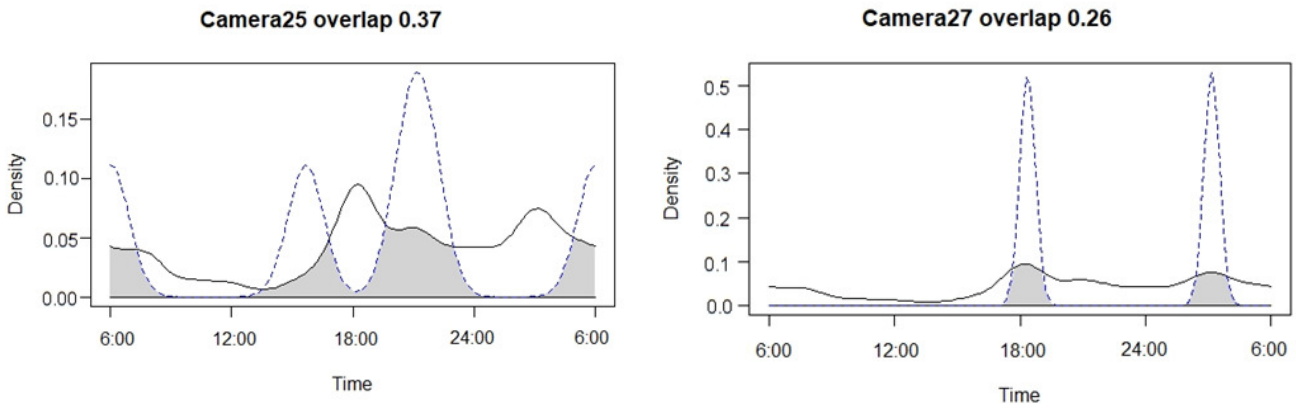


Figure 10. Unusual activity at six sites in relation to the overall winter activity of blacked-backed jackals at the Jackal Creek Golf Estate. The overlap coefficient (Δ) is the area under the minimum of two density estimates indicated by the grey area below curves, with the dotted line showing the site-specific activity and the solid line showing the overall winter activity (the scale of the graphs differs to accommodate different levels of activity at the different sites). The data were plotted using 'densityPlot'.

In the footage from site 7 (ENE of the Estate), an abnormally high peak in activity was noted just before 18h00 with no activity between 20h00 and 24h00, peaking excessively again at 01h30 and 03h00 with no activity after 04h00. Only travel was recorded from the footage at site 7, which could have contributed to the unusual peaks. At site 11 (NNE of the Estate), there was an increase in activity from 18h00, peaking at 20h00 and decreasing from 23h30 with low to no activity from 03h00 to 06h00. This differed from the overall activity pattern which showed a decrease in activity over the same period (21h00 to 24h00), and a peak in activity at 03h00. Travel was most commonly displayed at this site. Site 18 (SSW of the Estate) showed a peak in activity in the morning and afternoon, at 11h00 and 16h00 respectively, with little to no activity in the evening and nocturnally, between 19h00 and 06h00. Jackals mostly rested at this site. Footage at site 24 (NNW of the Estate) showed a peak in activity at midday, 12h00, and again at about 03h30. The behaviour in this footage was almost equally split between travel and forage. Foraging took place in the early morning, between 03h00 and 05h30, resulting in an activity peak at 03h30, whereas travelling took place during daylight hours, between 11h00 and 12h40, resulting in the peak at midday. Site 25 (WNW of the Estate) showed three peaks in activity with little to no activity between the peaks. The peaks occurred at 06h00, 15h00 and 21h00. Travel occurred predominantly at this site. Lastly, site 27 (NNW of the Estate) showed a peak in activity at 18h20 and again at

03h10. Although this appears to coincide with the overall activity pattern displayed, the peaks were excessively high. This is as a result of two videos captured with this camera, therefore contributing to the average activity pattern but being displayed as abnormal peaks.

In summer, the black-backed jackals displayed two peaks in activity, an extended evening crepuscular peak at 19h00 till 22h00 and a nocturnal peak at 04h00 (Figure 11). Overall, activity was lowest in the morning and low in the afternoon.

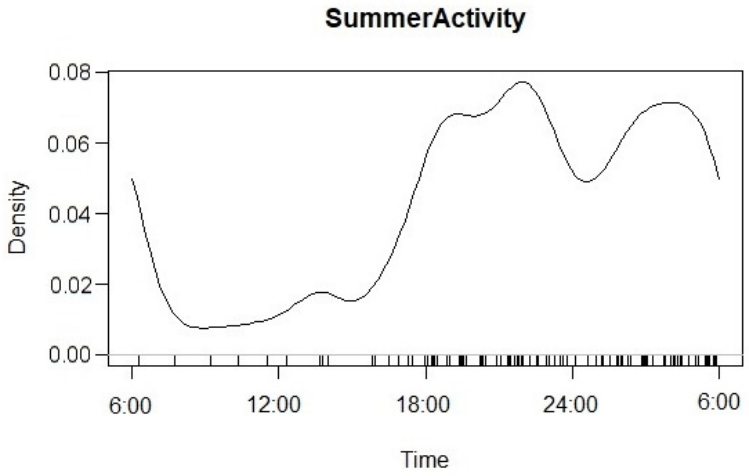


Figure 11. Overall summer activity displayed by the black-backed jackal at the Jackal Creek Golf Estate from camera-trap footage showing dusk and nocturnal peaks. The data was plotted using 'densityPlot'.

Site-specific differences in summer

Unusual activity was identified at six sites, determined by an overlap coefficient of less than 0.3, indicating that the overlap of activity at a particular site coincided with less than a third of the overall activity seen during summer; a lower overlap coefficient was used to capture more activity in summer because of fewer black-backed jackals on camera trap footage per site compared with winter. Unusual activity occurred at sites 1.1 (rotated view of site 1), 3, 5, 7, 16 and 33 (Figure 12).

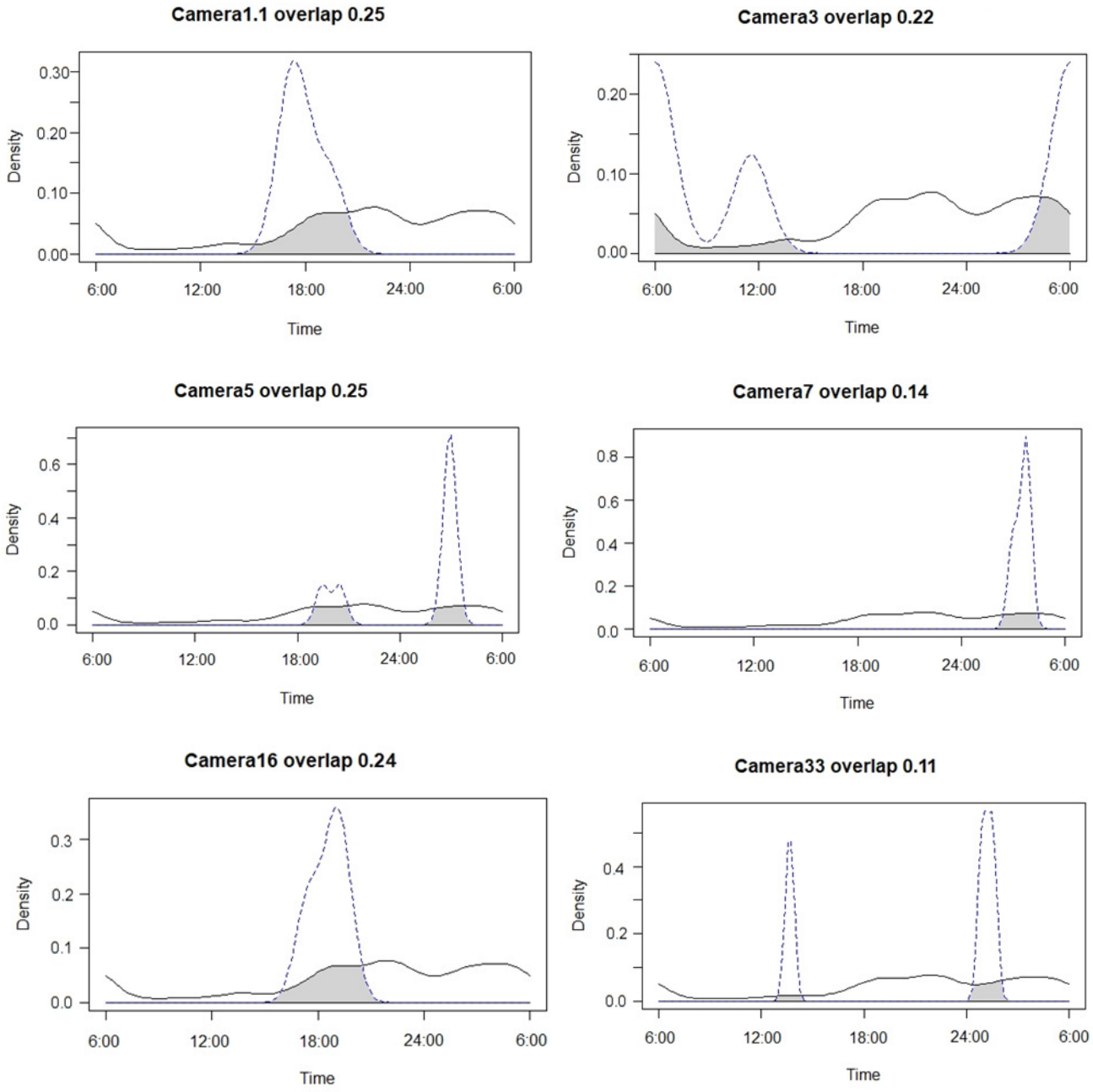


Figure 12. Activity at six sites showing unusual activity in relation to the overall summer activity of blacked-backed jackal at the Jackal Creek Golf Estate. The overlap coefficient (Δ) is the area under the minimum of two density estimates indicated by the grey area below curves, with the dotted line showing the site-specific activity and the solid line showing the overall summer activity (the scale of the graphs differs to accommodate different levels of activity at the different sites). The data were plotted using 'densityPlot'.

The footage from the camera at site 1.1 (NNW of the Estate) showed an unusually high peak in activity just before 18h00 with no activity at any other time of day. Site 3 (SSW

of the Estate) showed a midday peak and morning crepuscular activity (05h00 to 07h00). This differed from the overall activity pattern which showed a decrease in activity over the same period (06h00 to 14h00). However, few occurrences of black-backed jackals were captured by the camera at this site. Travel was again the most commonly displayed behaviour at this site. In the site 5 (SSE of the Estate) footage, an increase in activity around 19h00 was displayed, which is in accordance with the overall activity pattern for summer. However, it also showed a peak at 03h00, outside of the overall activity pattern for summer. The behaviours recorded in the second peak were travel and rest, perhaps showing the jackals resting before dawn, reducing activity slightly earlier than seen in the overall activity. Site 7 (ENE of the Estate) footage showed a peak in activity at 04h00. Travel was the predominant behaviour displayed in the few videos captured at this site. This peak in activity is in accordance with the overall activity pattern for summer but is considered unusual as a result of the lack of activity here during any other time period of the day. The footage from site 16 (NNW of the Estate) showed a peak in activity that presents as evening crepuscular activity. This unusual activity appears to be similar to that seen at site 7, with travel being the predominant behaviour displayed. The footage captured at this site was followed the overall activity pattern displayed for summer but showed a reduction in activity. Lastly, at site 33 (SSW of the Estate), there was a peak in activity at 13h30 and again at 01h15. This was as a result of only three videos with black-backed jackals captured at this site. The predominant behaviour displayed in the videos was travel.

A comparison of the overlap of winter and summer activity generated a coefficient of 0.84 (Figure 13). This suggests that there was not a large seasonal difference in the overall activity patterns displayed by the jackals. The peak activity times differed by one hour, with the winter peaks occurring an hour earlier than the summer peaks. Activity in both seasons was low in the afternoon and lower in summer than in winter.

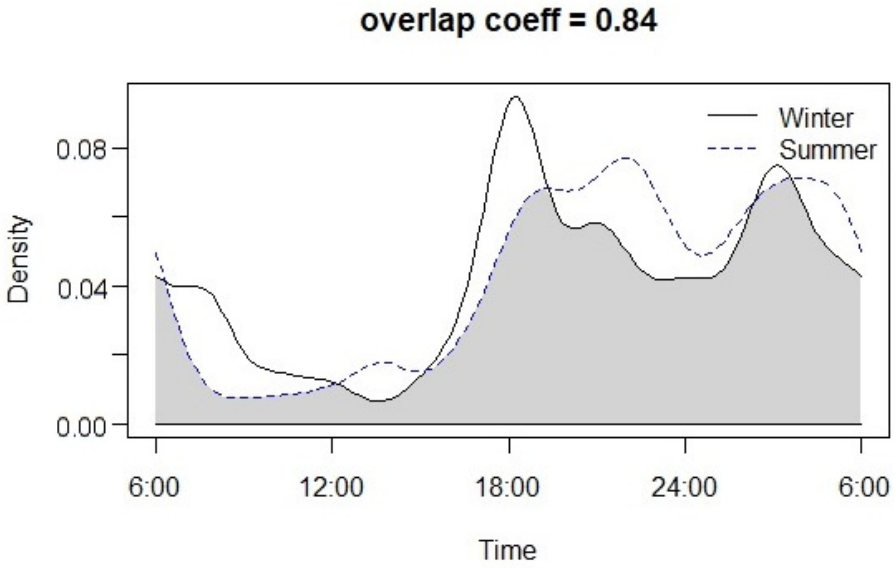
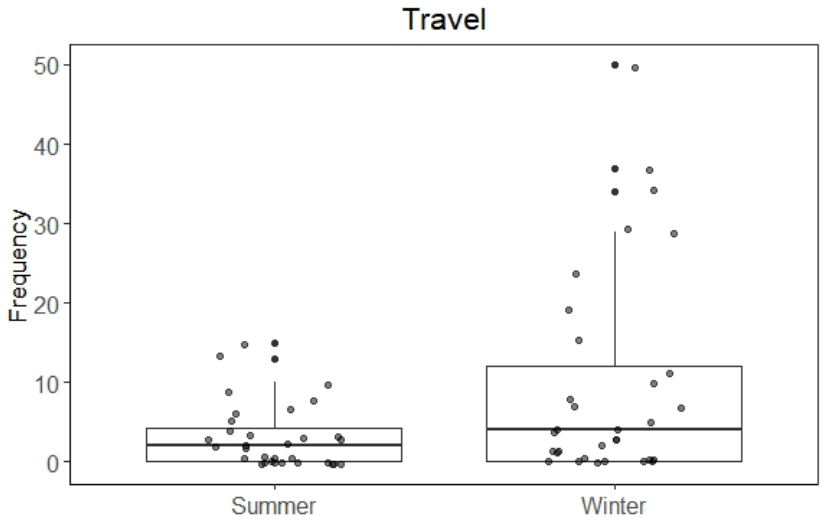


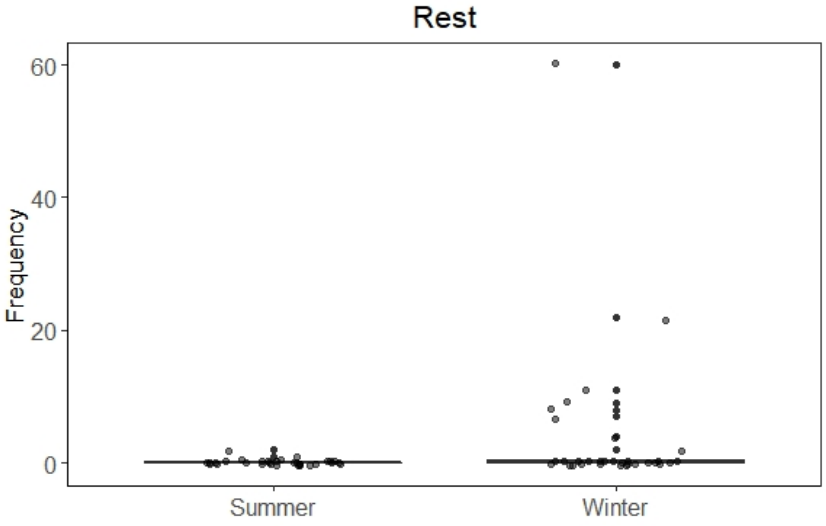
Figure 13. Comparison of the overall activity between winter and summer activity of blacked-backed jackals at the Jackal Creek Golf Estate. The overlap coefficient (Δ) is the area under the minimum of two density estimates indicated by the grey area below the curves.

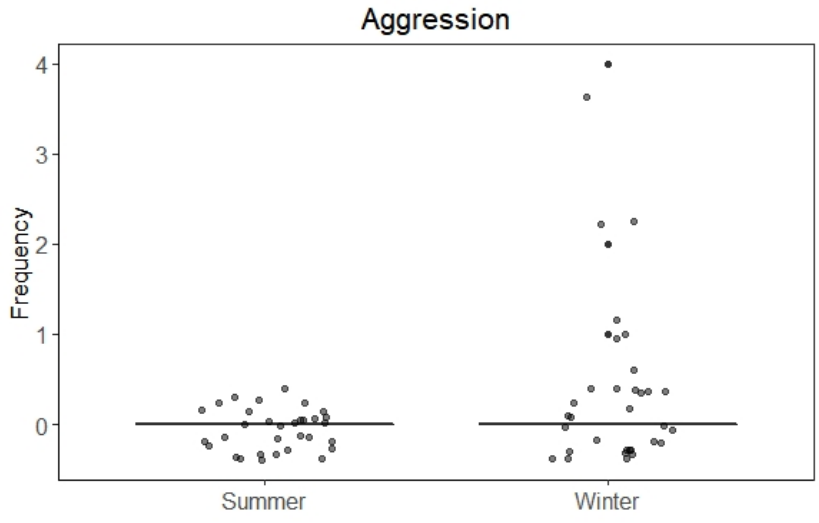
Behaviour

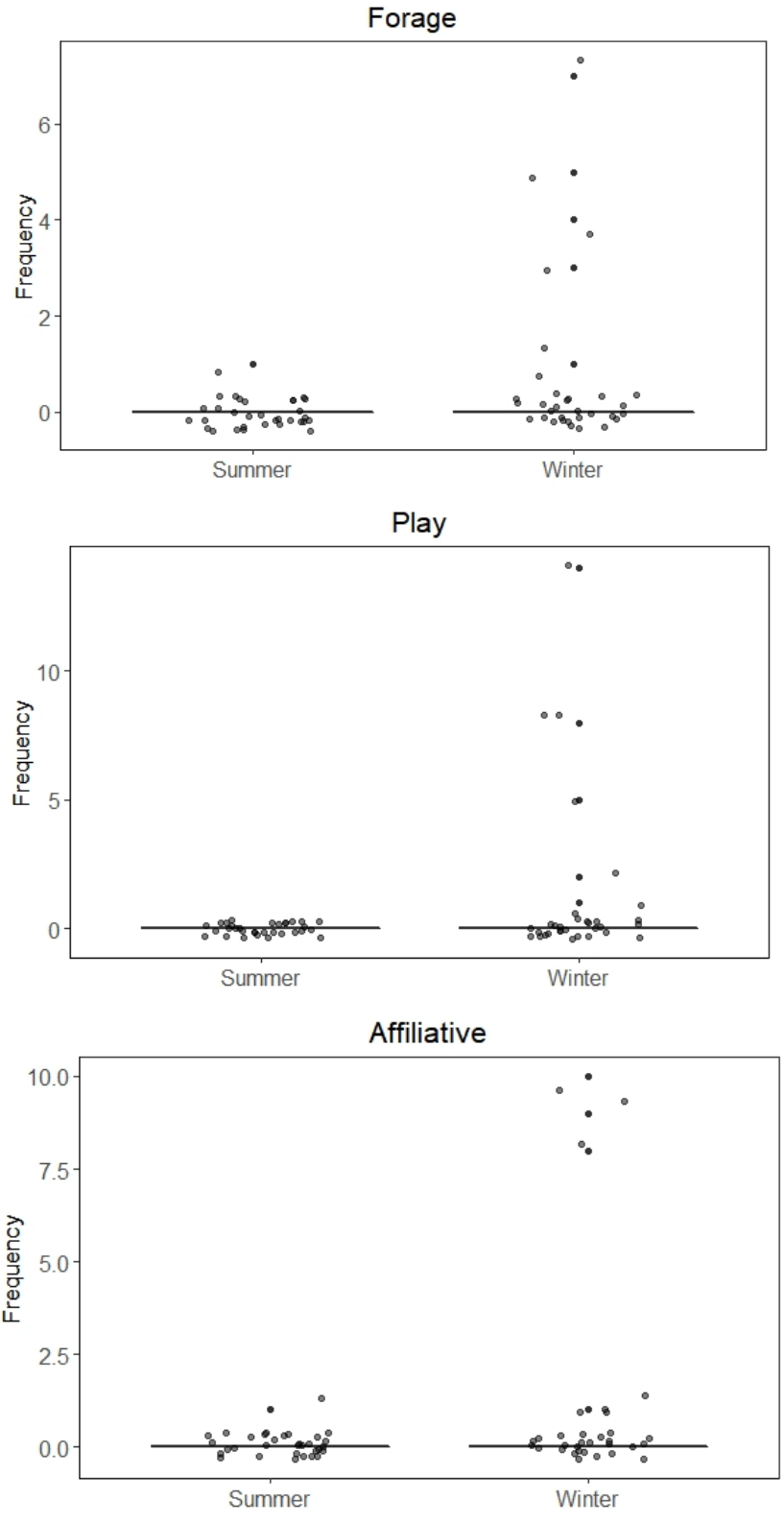
Travel and rest occurred most frequently in both seasons, followed by other behaviours occurring frequently in winter. The remaining behaviours, forage, play, affiliative and aggression occurred minimally or were absent in both seasons. Thus, statistical analyses were only possible for travel and rest. The remaining behaviours could not be analysed because of the low/zero values, as seen in Figure 14.

Travel occurred significantly more often in winter than in summer ($\beta = -1.38$, $\chi^2=16.71$, df=1, $p<0.001$). Rest also occurred significantly more often in winter than in summer ($\beta = -4.11$, $\chi^2=18.10$, df=1, $p<0.001$).


Travel
Frequency
50
40
30
20
10
0
Summer
Winter


Rest
Frequency
60
40
20
0
Summer
Winter


Aggression
Frequency
4
3
2
1
0
Summer
Winter


Forage
Frequency
6
4
2
0
Summer
Winter
Play
Frequency
10
5
0
Summer
Winter
Affiliative
Frequency
10.0
7.5
5.0
2.5
0.0
Summer
Winter

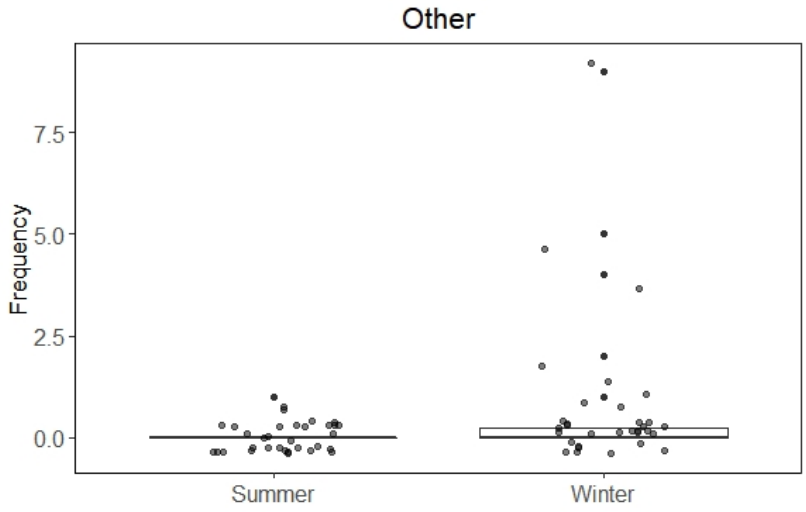


Figure 14. The frequencies of the black-backed jackal behaviours scored by season. Boxes indicate the inter-quartile range; whiskers indicate the maximum values of the data set and the black dots indicate outliers.

For the temporal analysis of the various behaviours, there was a significant difference in behaviour between seasons in time bracket Night (00h00 to 06h00) (χ^2=36.02; df=6; p<0.001) and time bracket Evening/Night (18h00 to 24h00) (χ^2=22.76; df=6; p=0.001). In the Night-time period, two behaviours, travel, and rest, had the highest contribution to the chi-squared analysis, both of which occurred significantly more often in winter than in summer (Figure 15) (Supplementary 1). In the Evening/Night, travel and rest again occurred significantly more often in winter than in summer (Figure 16).

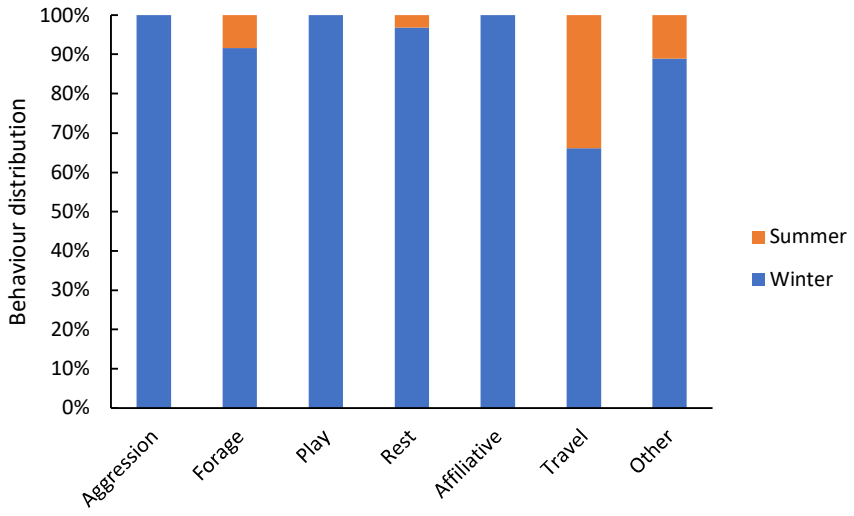


Figure 15. Percentage occurrence of seven behaviours by black-backed jackals for the Night (00h00 to 06h00) period in winter and summer at the Jackal Creek Golf Estate.

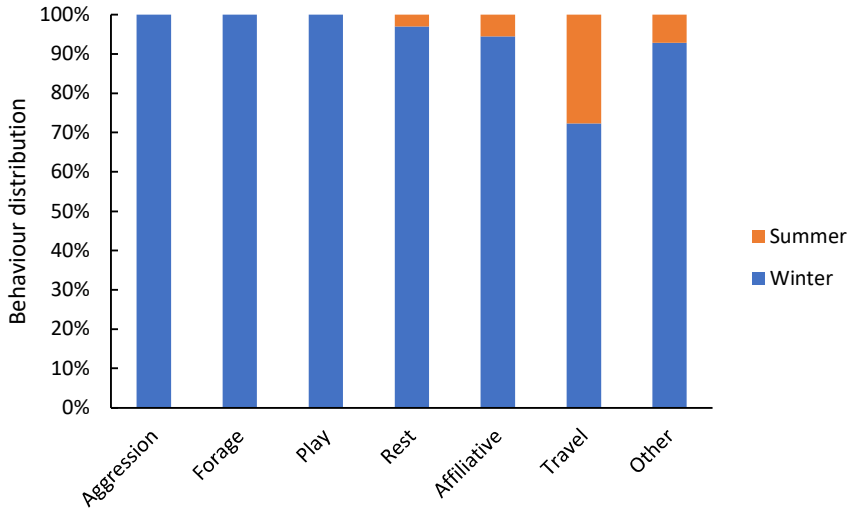


Figure 16. Percentage occurrence of seven behaviours by black-backed jackals for the Evening/Night (18h00 to 24h00) period in winter and summer at the Jackal Creek Golf Estate.

There were no significant seasonal differences in behaviour in the Morning (06h00 to 12h00) (χ^2=2.06; df=6; p=0.914) and Afternoon (12h00 to 18h00) (χ^2=4.48; df=5; p=0.483) periods (Supplementary 2). For the Afternoon time period, aggression was excluded from the analyses since none was recorded.

Analysis of behaviours by time period in winter

Comparisons of the occurrence of behaviours in four time periods are shown in Figure 17. The frequencies of behaviours differed significantly in the four periods defined in the study: Night (χ^2=186.51; df=6; p<0.001), Morning (χ^2=186.33; df=6; p<0.001), Afternoon (χ^2=230.00; df=6; p<0.001) and Evening/Night (χ^2=354.13; df=6; p<0.001).

All seven behaviours were recorded at Night. There was a graded response according to the outputs of pairwise comparisons: travel occurred significantly the most, followed by rest and play (Table 1).

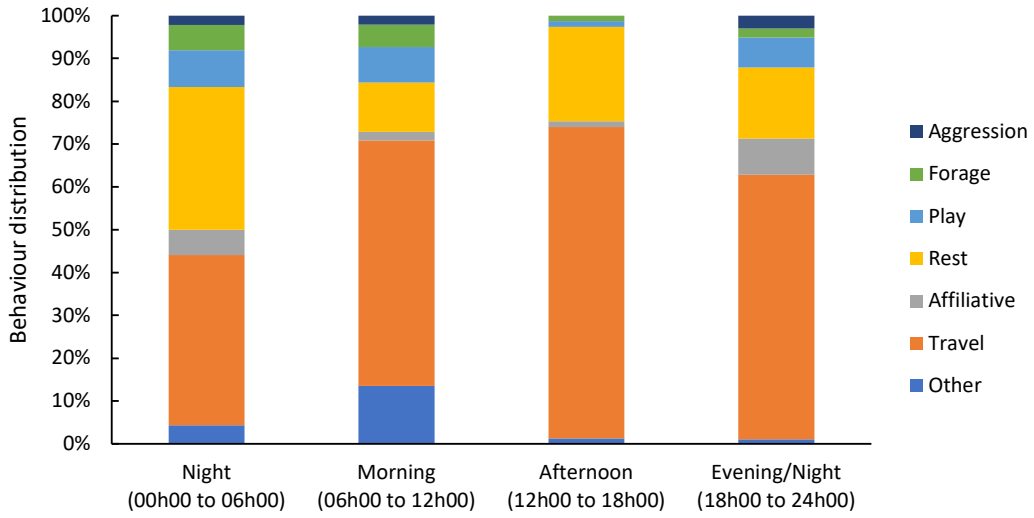


Figure 17. Percentage occurrence of seven behaviours by black-backed jackals for all time periods in winter at the Jackal Creek Golf Estate.

Table 1. Pairwise chi-squared comparisons between categories of behaviours by black-backed jackals at the Jackal Creek Golf Estate in the Night period in winter 2019. Df = 1 for all comparisons. Significant comparisons are shown in bold.

Comparison	χ^2 value	p-value
Travel vs. Rest	1.06	0.303
Travel vs. Forage	**46.69**	**<0.001**
Travel vs. Play	**37.38**	**<0.001**
Travel vs. Affiliative	**46.69**	**<0.001**
Travel vs. Aggression	**62.82**	**<0.001**
Travel vs. Other	**53.12**	**<0.001**
Rest vs. Forage	**35.63**	**<0.001**
Rest vs. Play	**27.13**	**<0.001**
Rest vs. Affiliative	**35.63**	**<0.001**
Rest vs. Aggression	**50.97**	**<0.001**
Rest vs. Other	**41.66**	**<0.001**
Forage vs. Play	0.93	0.336
Forage vs. Affiliative	0.00	1.000
Forage vs. Aggression	3.27	0.071
Forage vs. Other	0.47	0.491
Play vs. Affiliative	0.93	0.336
Play vs. Aggression	**7.20**	**0.007**
Play vs. Other	2.67	0.102
Affiliative vs. Aggression	3.27	0.071

Affiliative vs. Other	0.47	0.491
Aggression vs. Other	1.33	0.248

All seven behaviours were recorded in the Morning time bracket. There was a graded response according to the outputs of pairwise comparisons: travel occurred significantly the most, followed by rest and play (Table 2).

Table 2. Pairwise chi-squared comparisons between categories of behaviours by black-backed jackals at the Jackal Creek Golf Estate in the Morning period in winter 2019. Df = 1 for all comparisons. Significant comparisons are shown in bold.

Comparison	χ^2 value	p-value
Travel vs. Rest	**29.33**	**<0.001**
Travel vs. Forage	**41.67**	**<0.001**
Travel vs. Play	**35.06**	**<0.001**
Travel vs. Affiliative	**49.28**	**<0.001**
Travel vs. Aggression	**49.28**	**<0.001**
Travel vs. Other	**52.07**	**<0.001**
Rest vs. Forage	2.25	0.134
Rest vs. Play	0.47	0.491
Rest vs. Affiliative	**6.23**	**0.013**
Rest vs. Aggression	**6.23**	**0.013**
Rest vs. Other	**8.33**	**0.004**
Forage vs. Play	0.69	0.405
Forage vs. Affiliative	1.29	0.257
Forage vs. Aggression	1.29	0.257
Forage vs. Other	2.67	0.102
Play vs. Affiliative	3.60	0.058
Play vs. Aggression	3.60	0.058
Play vs. Other	**5.44**	**0.020**
Affiliative vs. Aggression	0.00	1.000
Affiliative vs. Other	0.33	0.564
Aggression vs. Other	0.33	0.564

In the Afternoon period, all behaviours except aggression were recorded. A graded response in the outputs of pairwise comparisons showed that travel occurred significantly the most, followed by rest (Table 3).

Table 3. Pairwise chi-squared comparisons between categories of behaviours by black-backed jackals at the Jackal Creek Golf Estate in the Afternoon period in winter 2019. Df = 1 for all comparisons. Significant comparisons are shown in bold.

Comparison	χ^2 value	p-value
Travel vs. Rest	**20.84**	**<0.001**
Travel vs. Forage	**53.07**	**<0.001**
Travel vs. Play	**53.07**	**<0.001**
Travel vs. Affiliative	**53.07**	**<0.001**
Travel vs. Other	**50.28**	**<0.001**
Rest vs. Forage	**14.22**	**<0.001**
Rest vs. Play	**14.22**	**<0.001**
Rest vs. Affiliative	**14.22**	**<0.001**
Rest vs. Other	**11.84**	**0.001**
Forage vs. Play	0.00	1.000
Forage vs. Affiliative	0.00	1.000
Forage vs. Other	0.33	0.564
Play vs. Affiliative	0.00	1.000
Play vs. Other	0.33	0.564
Affiliative vs. Other	0.33	0.564

All behaviours were recorded in the Evening/Night period. Again, there was a graded response according to the outputs of pairwise comparisons: travel occurred significantly the most, followed by rest, affiliative and, play and other behaviours equally (Table 4).

Table 4. Pairwise chi-squared comparisons between categories of behaviours by black-backed jackals at the Jackal Creek Golf Estate in the Evening/Night period in winter 2019. Df = 1 for all comparisons. Significant comparisons are shown in bold.

Comparison	χ^2 value	p-value
Travel vs. Rest	**51.92**	**<0.001**
Travel vs. Forage	**111.50**	**<0.001**
Travel vs. Play	**86.72**	**<0.001**
Travel vs. Affiliative	**80.26**	**<0.001**
Travel vs. Aggression	**106.12**	**<0.001**
Travel vs. Other	**88.97**	**<0.001**
Rest vs. Forage	**22.73**	**<0.001**
Rest vs. Play	**7.68**	**0.006**
Rest vs. Affiliative	**5.12**	**0.024**
Rest vs. Aggression	**18.69**	**0.000**
Rest vs. Other	**8.70**	**0.003**

Forage vs. Play	**5.56**	**0.018**
Forage vs. Affiliative	**8.05**	**0.005**
Forage vs. Aggression	0.40	0.527
Forage vs. Other	**4.76**	**0.029**
Play vs. Affiliative	0.29	0.590
Play vs. Aggression	3.20	0.074
Play vs. Other	0.04	0.847
Affiliative vs. Aggression	**5.26**	**0.022**
Affiliative vs. Other	0.53	0.465
Aggression vs. Other	2.58	0.108

Analysis of behaviours by time period in summer

Comparisons of the occurrence of behaviours in four time periods is shown in Figure 18. Two of the four time periods showed significant differences: Night (χ^2=199.67; df=6; p<0.001) and Evening/Night (χ^2=259.68; df=6; p<0.001). No statistical analysis was possible for the behaviours in the Morning and Afternoon periods since only travel was recorded in these time periods.

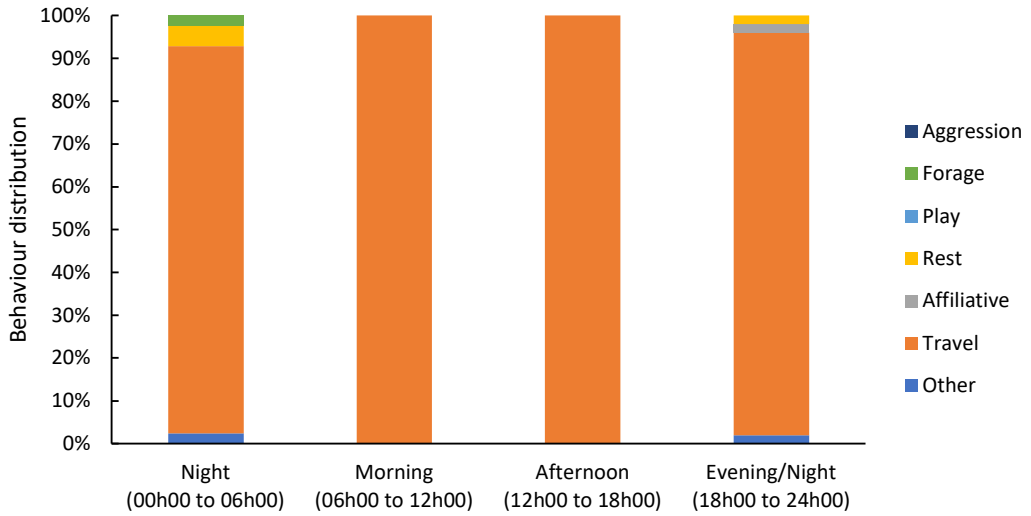


Figure 18. Percentage occurrence of seven behaviours by black-backed jackals for all time periods in summer at the Jackal Creek Golf Estate.

The behaviours recorded in the Night were travel, rest, forage and other with travel occurring significantly more often than rest, forage and other (Table 5).

Table 5. Pairwise chi-squared comparisons between categories of behaviours by black-backed jackals at the Jackal Creek Golf Estate in the Night period in summer 2019/2020. Df = 1 for all comparisons. Significant comparisons are shown in bold.

Comparison	χ^2 value	p-value
Travel vs. Rest	**32.40**	**<0.001**
Travel vs. Forage	**35.10**	**<0.001**
Travel vs. Other	**35.10**	**<0.001**
Rest vs. Forage	0.33	0.564
Rest vs. Other	0.33	0.564
Forage vs. Other	0.00	1.000

In the Evening/Night, travel, rest, affiliative and other behaviours were recorded, with travel occurring significantly more often than rest, affiliative and other (all comparisons were $p<0.001$).

Analysis of behaviour in winter with regard to location

Analysis of behaviours by location

Comparisons of the frequency of occurrence of behaviours by location (cardinal zones) are shown in Figure 19. Of the eight zones, significant differences between behaviours occurred in each of five zones: ENE (χ^2=142.54; df=6; $p<0.001$), SSW (χ^2=286.50; df=6; $p<0.001$), WSW (χ^2=106.46; df=6; $p<0.001$), WNW (χ^2=44.00; df=6; $p<0.001$) and NNW (χ^2=355.50; df=6; $p<0.001$). No statistical analysis was possible for the behaviours in the SSE, NNE, and ESE zones since only travel was recorded in these zones.

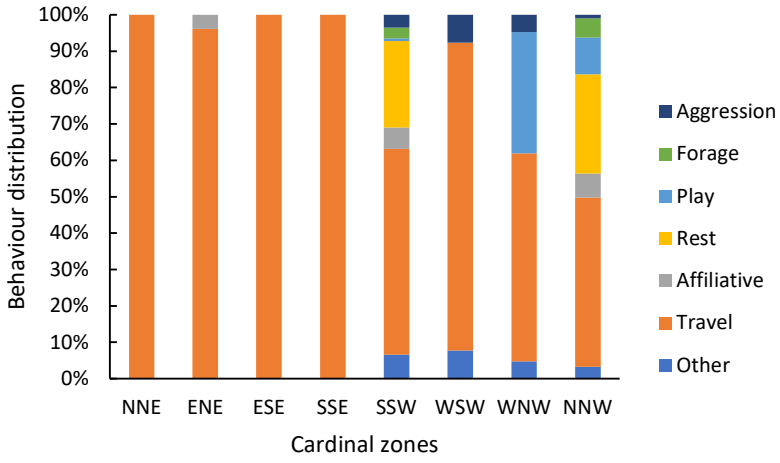


Figure 19. Percentage occurrence of seven behaviours by black-backed jackals for the cardinal zones in winter at the Jackal Creek Golf Estate.

In the ENE zone, pairwise comparisons could only be done between travel and affiliative behaviours since these were the only behaviours that were recorded in this zone. Travel occurred significantly more often than affiliative behaviour (χ^2=22.15; df=1; p<0.001). In the SSW zone, there was a graded response according to the outputs of pairwise comparisons: travel occurred significantly the most, followed by rest and, affiliative and other behaviours equally (Table 6).

Table 6. Pairwise chi-squared comparisons between categories of behaviours by black-backed jackals at the Jackal Creek Golf Estate in the SSW zone of the Estate in winter 2019. Df = 1 for all comparisons. Significant comparisons are shown in bold.

Comparison	χ^2 value	p-value
Travel vs. Rest	**22.41**	**<0.001**
Travel vs. Forage	**81.00**	**<0.001**
Travel vs. Play	**92.04**	**<0.001**
Travel vs. Affiliative	**68.81**	**<0.001**
Travel vs. Aggression	**78.43**	**<0.001**
Travel vs. Other	**66.57**	**<0.001**
Rest vs. Forage	**27.22**	**<0.001**
Rest vs. Play	**37.10**	**<0.001**
Rest vs. Affiliative	**18.00**	**<0.001**
Rest vs. Aggression	**25.13**	**<0.001**
Rest vs. Other	**16.49**	**<0.001**
Forage vs. Play	2.67	0.102
Forage vs. Affiliative	1.67	0.197
Forage vs. Aggression	0.09	0.763

Forage vs. Other	2.25	0.134
Play vs. Affiliative	**7.36**	**0.007**
Play vs. Aggression	3.57	0.059
Play vs. Other	**8.33**	**0.004**
Affiliative vs. Aggression	1.00	0.317
Affiliative vs. Other	0.05	0.827
Aggression vs. Other	1.47	0.225

In the WSW zone, travel, aggression, and other behaviours were recorded, with travel occurring significantly more often than aggression and other behaviours (both comparisons were $p<0.001$). In the WNW zone, travel, play, aggression, and other behaviours were recorded. Travel occurred significantly more often than both aggression and other behaviours equally ($\chi^2=9.31$; df=1; $p=0.002$). Play occurred significantly more often than both aggression and other behaviours equally ($\chi^2=4.50$; df=1; $p=0.034$). All seven behaviours were recorded in the NNW zone. There was a graded response according to the outputs of pairwise comparisons: travel occurred significantly the most, followed by rest, play, forage and affiliative equally and lastly aggression (Table 7).

Table 7. Pairwise chi-squared comparisons between categories of behaviours by black-backed jackals at the Jackal Creek Golf Estate in the NNW zone of the Estate in winter 2019. Df = 1 for all comparisons. Significant comparisons are shown in bold.

Comparison	χ^2 value	p-value
Travel vs. Rest	**15.47**	**<0.001**
Travel vs. Forage	**100.48**	**<0.001**
Travel vs. Play	**71.22**	**<0.001**
Travel vs. Affiliative	**91.88**	**<0.001**
Travel vs. Aggression	**133.25**	**<0.001**
Travel vs. Other	**114.63**	**<0.001**
Rest vs. Forage	**45.34**	**<0.001**
Rest vs. Play	**23.72**	**<0.001**
Rest vs. Affiliative	**38.53**	**<0.001**
Rest vs. Aggression	**74.42**	**<0.001**
Rest vs. Other	**57.30**	**<0.001**
Forage vs. Play	**4.79**	**0.029**
Forage vs. Affiliative	0.44	0.505
Forage vs. Aggression	**8.89**	**0.003**
Forage vs. Other	1.38	0.239
Play vs. Affiliative	2.37	0.123

Play vs. Aggression	**23.06**	**<0.001**
Play vs. Other	**10.76**	**0.001**
Affiliative vs. Aggression	**12.57**	**<0.001**
Affiliative vs. Other	3.33	0.068
Aggression vs. Other	3.77	0.052

Analysis of each behaviour by all locations

Comparisons of behaviours by cardinal zones is presented in Figure 19. Travel was recorded in all zones, occurring more frequently in some zones than others. Most of the other behaviour types occurred in the western parts of the Estate. There was a graded response in the occurrence of travel across the cardinal zones according to the outputs of pairwise comparisons (χ^2=484.94; df=7; p<0.001): travel occurred significantly the most in the NNW zone, followed by the SSW, ENE, WSW and, WNW and SSE zones equally (Table 8).

Table 8. Pairwise chi-squared comparisons of travel behaviour by black-backed jackals at the Jackal Creek Golf Estate between zones in winter 2019. Df = 1 for all comparisons. Significant comparisons are shown in bold.

Comparison	χ^2 value	p-value
ENE vs. ESE	**22.15**	**<0.001**
ENE vs. NNE	**19.59**	**<0.001**
ENE vs. NNW	**81.97**	**<0.001**
ENE vs. SSE	**7.53**	**0.006**
ENE vs. SSW	**40.83**	**<0.001**
ENE vs. WNW	**4.57**	**0.033**
ENE vs. WSW	0.19	0.662
ESE vs. NNE	0.33	0.564
ESE vs. NNW	**139.03**	**<0.001**
ESE vs. SSE	**6.40**	**0.011**
ESE vs. SSW	**92.04**	**<0.001**
ESE vs. WNW	**9.31**	**0.002**
ESE vs. WSW	**19.17**	**<0.001**
NNE vs. NNW	**136.11**	**<0.001**
NNE vs. SSE	**4.45**	**0.035**
NNE vs. SSW	**89.16**	**<0.001**
NNE vs. WNW	**7.14**	**0.008**
NNE vs. WSW	**16.67**	**<0.001**
NNW vs. SSE	**117.15**	**<0.001**

NNW vs. SSW	**9.32**	**0.002**
NNW vs. WNW	**109.74**	**<0.001**
NNW vs. WSW	**87.80**	**<0.001**
SSE vs. SSW	**71.12**	**<0.001**
SSE vs. WNW	0.43	0.513
SSE vs. WSW	**5.45**	**0.020**
SSW vs. WNW	**64.38**	**<0.001**
SSW vs. WSW	**45.55**	**<0.001**
WNW vs. WSW	2.94	0.086

Rest was recorded only in the NNW and SSW zones of the Estate, occurring significantly more often in the NNW (χ^2=15.03; df=1; p<0.001). Forage was recorded in only the NNW and SSW zones, occurring significantly more often in the NNW (χ^2=5.76; df=1; p=0.016). Play was recorded in the NNW, SSW and WNW zones. In these zones, play occurred significantly more often in the NNW zone than both the SSW (χ^2=28.13; df=1; p<0.001) and WNW (χ^2=15.16; df=1; p<0.001) zones.

Most of the affiliative behaviour was recorded in the NNW and SSW zones, and minimally in the ENE zone. Affiliative behaviour occurred significantly more often in the NNW and SSW zones than in the ENE zone (χ^2=17.19; df=1; p<0.001) and (χ^2=7.36; df=1; p=0.007). Aggression occurred in the NNW, SSW, WNW, and WSW zones of the Estate. There was no significant difference in the occurrence of aggression in these zones.

Other behaviours were recorded in the NNW, SSW, WNW, and WSW zones of the Estate. A significant difference in other behaviours was recorded in the NNW compared to the WNW (χ^2=7.36; df=1; p=0.007) and the WSW (χ^2=5.33; df=1; p=0.021) zones. Other behaviours also occurred significantly more often in the SSW zone than the WNW (χ^2=8.33; df=1; p=0.004) and WSW (χ^2=6.23; df=1; p=0.013) zones.

The correlation between the frequency of travel in the various cardinal zones combined vs. the number of black-backed jackal sightings in these zones was significantly positive (r_s=1.00; p<0.001) (Figure 20). Similarly, the frequency of rest in the various cardinal zones combined vs. the number of black-backed jackal sightings in the same zones was significantly positive (r_s=0.76; S=19.84; p=0.027) (Figure 21). These outcomes indicate that the frequency of occurrence of these behaviours was a function of the number of sightings. Regressions were only determined for travel and rest due to the low frequency of occurrence of all other behaviours.

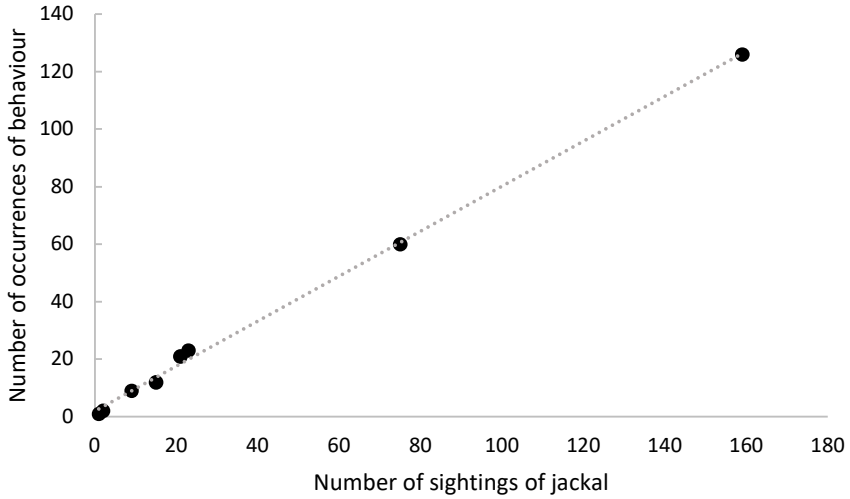


Figure 20. Relationship between the frequency of travel and the number of black-backed jackal sightings at the Jackal Creek Golf Estate for all zones combined in winter. The regression line is significant ($p<0.001$)

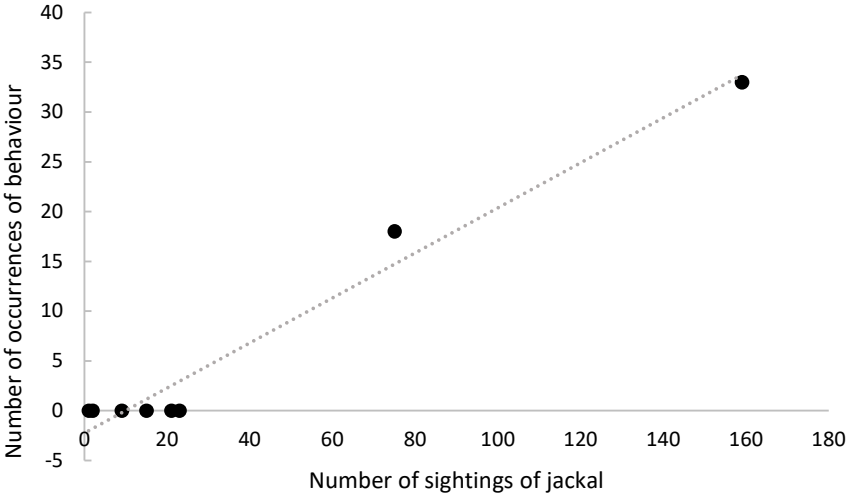


Figure 21. Relationship between the frequency of travel and the number of black-backed jackal sightings at the Jackal Creek Golf Estate for all zones combined in winter. The regression line is significant ($p=0.027$).

Analysis of behaviour in summer with regard to location

Analysis of behaviour by location

Comparisons of the frequency of occurrence of behaviours by location (cardinal zones) (Figure 22). Of the eight zones, significant behavioural differences occurred in each of five zones: NNE ($\chi^2=148.52$; df=6; $p<0.001$), SSE ($\chi^2=18.25$; df=6; $p<0.001$), WSW

(χ^2=47.40; df=6; p<0.001), WNW (χ^2=30.00; df=6; p<0.001) and NNW (χ^2=130.58; df=6; p<0.001). No statistical analysis was conducted in the ENE, SSW and ESE zones since only travel was recorded in these zones.

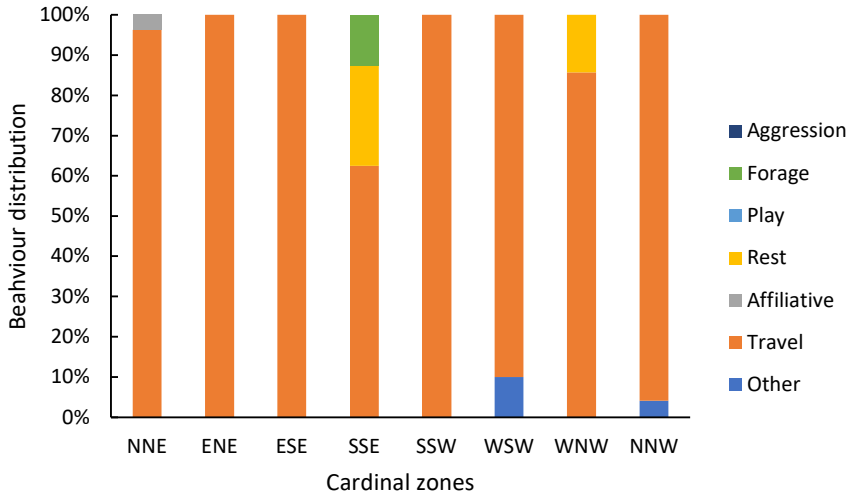


Figure 22. The Percentage occurrence of seven behaviours by black-backed jackals for the cardinal zones in summer at the Jackal Creek Golf Estate.

In the NNE zone, only travel and affiliative behaviours were recorded, with travel occurring significantly more often than affiliative behaviour (χ^2=23.15; df=1; p<0.001). Only travel and other behaviours were recorded in the NNW zone, with travel occurring significantly more often than other behaviours (χ^2=20.17; df=1; p<0.001). The behaviours recorded in the SSE zone were travel, rest, and forage. There was no significant difference in the occurrence of either of these behaviours in this zone. In the WNW zone, only travel and rest were recorded, which did not differ significantly from each other. Travel and other behaviours were recorded in the WSW zone, with travel occurring significantly more often than other behaviours (χ^2=6.40; df=1; p=0.011).

Analysis of each behaviour by all locations

Comparisons of behaviours by cardinal zones is presented in Figure 22. Travel was recorded in all zones, occurring more frequently in some zones than others. Most of the travel in summer occurred in the northern parts of the Estate. The occurrence of travel in summer also varied significantly by cardinal zones according to a graded response with regard to the outputs of pairwise comparisons (χ^2=38.64; df=7; p<0.001): travel occurred significantly the most in the NNE zone, followed by the NNW, ENE and SSW zones (Table 9).

Table 9. Pairwise chi-squared comparisons of travel behaviour by black-backed jackals at the Jackal Creek Golf Estate between zones in summer 2019/2020. Df = 1 for all comparisons. Significant comparisons are shown in bold.

Comparison	χ^2 value	p-value
ENE vs. ESE	**7.20**	**0.007**
ENE vs. NNE	2.38	0.123
ENE vs. NNW	1.26	0.262
ENE vs. SSE	**5.76**	**0.016**
ENE vs. SSW	0.57	0.450
ENE vs. WNW	**4.55**	**0.033**
ENE vs. WSW	1.96	0.162
ESE vs. NNE	**16.13**	**<0.001**
ESE vs. NNW	**13.37**	**<0.001**
ESE vs. SSE	0.11	0.739
ESE vs. SSW	**4.00**	**0.046**
ESE vs. WNW	0.40	0.527
ESE vs. WSW	1.92	0.166
NNE vs. NNW	0.18	0.668
NNE vs. SSE	**14.23**	**<0.001**
NNE vs. SSW	**5.16**	**0.023**
NNE vs. WNW	**12.50**	**<0.001**
NNE vs. WSW	**8.26**	**0.004**
NNW vs. SSE	**11.57**	**0.001**
NNW vs. SSW	3.46	0.063
NNW vs. WNW	**9.97**	**0.002**
NNW vs. WSW	**6.13**	**0.013**
SSE vs. SSW	2.88	0.090
SSE vs. WNW	0.09	0.763
SSE vs. WSW	1.14	0.285
SSW vs. WNW	2.00	0.157
SSW vs. WSW	0.43	0.513
WNW vs. WSW	0.60	0.439

The occurrence of the remaining behaviours was minimal throughout the Estate in summer. Rest was only recorded in the SSE and WNW zones of the Estate. Forage was recorded only in the SSE zone, and affiliative only in the NNE zone. Other behaviours were recorded in the NNW and WSW zones. Play and aggression were not recorded in any zone during the summer sampling.

The correlation between the frequency of travel in the various cardinal zones combined vs. the number of black-backed jackal sightings in the zones was not statistically significant (r_s=0.40; S=49.98; p=0.320) (Figure 23). The correlation between the frequency of rest in the various cardinal zones combined vs. the number of black-backed jackal sightings in the zones was significantly positive (r_s=0.76; S=20.12; p=0.028) (Figure 24). Regressions were only determined for travel and rest due to the low frequency of occurrence of all other behaviours.

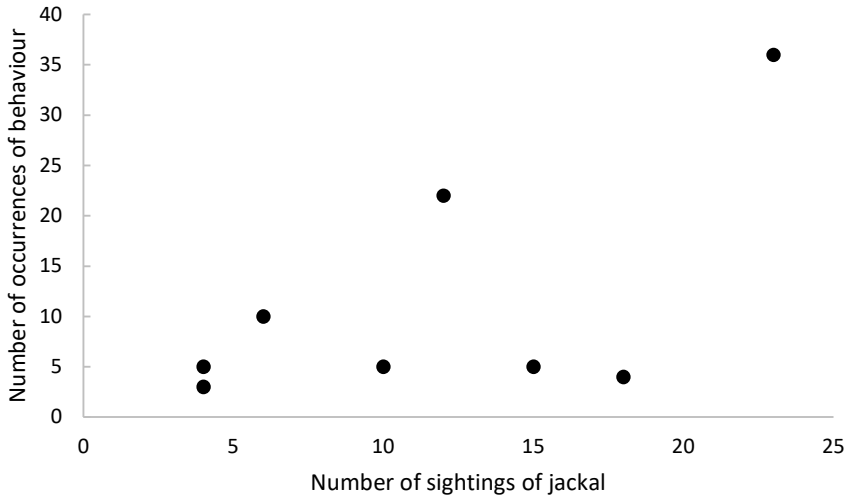


Figure 23. Relationship between frequency of travel and the number of black-backed jackal sightings at the Jackal Creek Golf Estate for all zones combined in summer. The regression was not significant (p=0.320) and therefore a regression line is not provided.

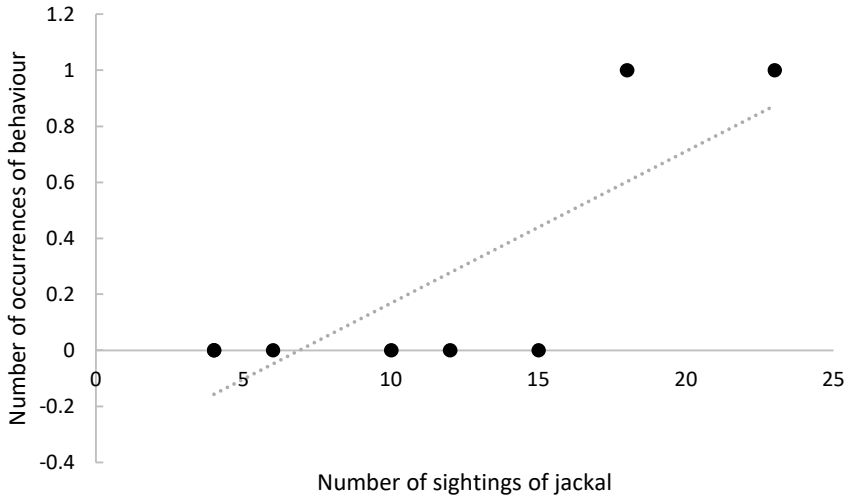


Figure 24. Relationship between rest and the number of black-backed jackal sightings at the Jackal Creek Golf Estate for all zones combined in summer. The regression line is significant (p=0.028).

Scat components

Forty-three scats were collected at the Estate during June, July, and August 2019, in order to assess the winter diet of the black-backed jackals and twenty-seven scats were collected during December 2019, January and February 2020 to assess their summer diet. The scat analysis showed a wide variety of components in nine categories: mammals, birds, arthropods, unidentifiable vertebrates, monocotyledonous plants, dicotyledonous plants, fruits and seeds, anthropogenic matter, and other unidentifiable components (Table 10). In both seasons, the Simpson's diversity index was 0.88 according to the number of occurrences of categories in the scats, and Levin's standardized index was 0.91. These results indicate a large degree of diversity in the diet and a generalist diet. Diversity indices are used as a metric assessment of diet breadth.

Table 10. Number of occurrences (N), frequency of occurrence (%O), numerical frequency of occurrence (%N) and percentage mass contribution (%M) for each component in the scat (n = 70) of black-backed jackals at the Jackal Creek Golf Estate.

	Winter				**Summer**			
Scat components	**(n = 43)**				**(n = 27)**			
	N	**%O**	**%N**	**%M**	**N**	**%O**	**%N**	**%M**
Mammals	20	46.5	9.1	3.8	10	37.0	7.8	2.7
Birds	18	41.9	8.2	1.3	13	48.1	10.2	1.0
Arthropods	14	32.6	6.4	0.6	16	59.3	12.5	1.3
Unidentifiable vertebrates	28	65.1	12.7	6.7	19	70.4	14.8	11.9
Monocots	41	95.3	18.6	1.4	23	85.2	18.0	0.4
Dicots	32	74.4	14.5	0.3	15	55.6	11.7	0.2
Fruits/Seeds	16	37.2	7.3	0.4	10	37.0	7.8	0.1
Anthropogenic	20	46.5	9.1	4.6	12	44.4	9.4	2.6
Other unidentifiable	31	72.1	14.1	1.0	10	37.0	7.8	0.2

Ranking the components using the results in Table 10 indicated that monocotyledonous plants occurred more often in both winter and summer according to the

frequency of occurrence and numerical frequency (Table 11). According to percentage mass contribution, unidentifiable vertebrates were ranked highest, occurring more often in both seasons (Table 11).

Table 11. The rank of each scat components (1 being the highest ranked and 9 being the lowest) for the three methods of analysis (frequency of occurrence (%O), numerical frequency of occurrence (%N) and percentage mass contribution (%M)) found in the scat (n = 70) of black-backed jackals at the Jackal Creek Golf Estate.

	Winter			**Summer**		
Scat components	**(n = 43)**			**(n = 27)**		
	%O	**%N**	**%M**	**%O**	**%N**	**%M**
Mammals	5	5	3	7	7	2
Birds	6	6	5	5	5	5
Arthropods	8	8	7	3	3	4
Unidentifiable vertebrates	4	4	**1**	2	2	**1**
Monocots	**1**	**1**	4	**1**	**1**	6
Dicots	2	2	9	4	4	7
Fruits/seeds	7	7	8	7	7	8
Anthropogenic	5	5	2	6	6	3
Other unidentifiable	3	3	6	7	7	7

Winter vs. summer scat analyses

Seasonal comparison of scat components of the black-backed jackals showed no significant difference with regards to numerical frequency (χ^2=4.61, df=8, p=0.799) (Supplementary 3) and percentage mass contribution (χ^2=3.94, df=8, p=0.863) (Supplementary 4). However, there was a significant difference in the frequency of occurrence of scat components in winter compared with summer (χ^2=22.70; df=8; p=0.004) (Supplementary 5). Pairwise comparisons indicated that arthropods occurred significantly more often in the scat in summer than winter (χ^2=7.76; df=1; p=0.005), and other

unidentifiable components occurred significantly more often in winter than summer (χ^2=11.26; df=1; p=0.001) (Figure 25) (Supplementary 6).

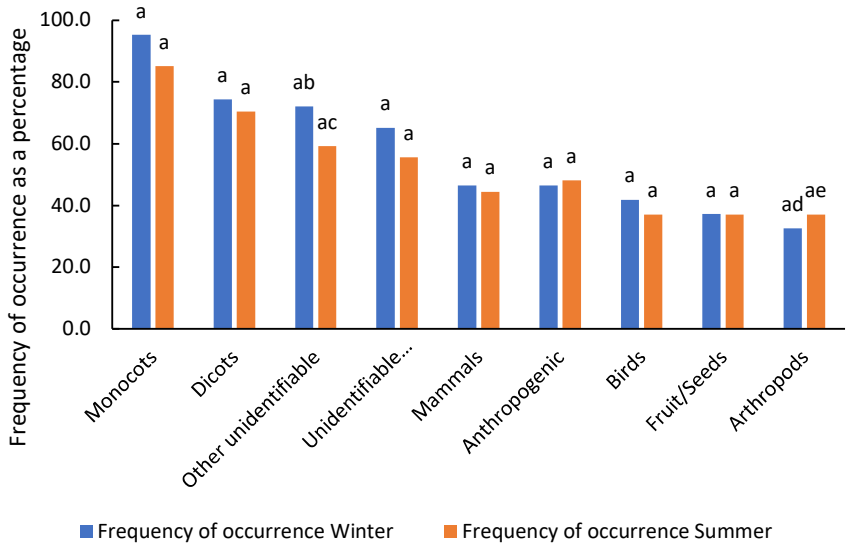


Figure 25. The frequency of occurrence of scat components of the black-backed jackals during winter and summer at the Jackal Creek Golf Estate. For each component bars with different alphabets indicate significant differences.

The GPS locations of the scat samples collected in winter showed a clustering of samples in the North and South of the Estate, with scat that contained anthropogenic matter being neither particularly close to nor far away from the human residences (Figure 26). The GPS locations of the scat samples collected in summer again showed a clustering of samples in the North and South of the Estate, with scat that contained anthropogenic matter being neither particularly close to nor far away from the human residences (Figure 26).

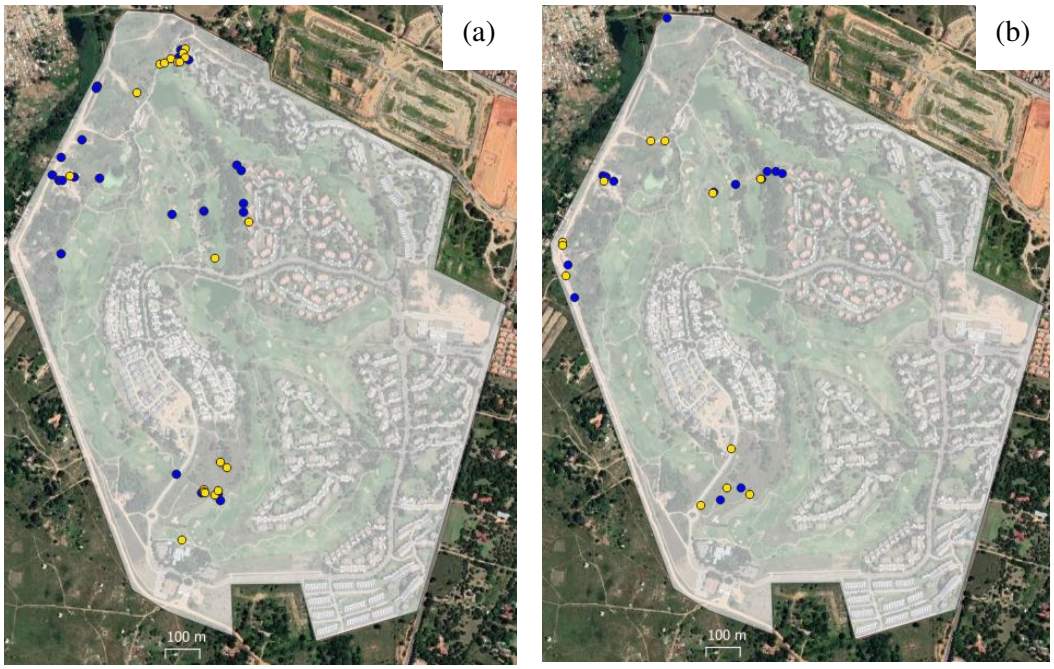


Figure 26. Locations of black-backed scat samples collected at the Jackal Greek Golf Estate in (a) winter 2019 and (b) summer 2019/2020. The Estate is shown as a faded outline. For both seasons, yellow dots represent samples in which anthropogenic items were present and blue dots represent samples with no anthropogenic content.

Winter samples

In winter, monocotyledonous plants were the most commonly occurring components, occurring in 95.3% of scats. Dicotyledonous plants and other unidentifiable matter occurred in similar quantities, occurring in 74.4% and 72.1% of scats, respectively. The least frequently occurring components were fruits and seeds and arthropods, occurring in 37.2% and 32.6% of scats, respectively. The frequency of occurrence of the various scat components in winter differed significantly from chance (i.e. a null model; χ^2=61.67; df=8; p<0.001). Similarly, the percentage mass contribution of the scat components differed significantly from chance (χ^2=18.29; df=8; p=0.019). However, for numerical frequency, there was no significant difference between the components (χ^2=12.05; df=8; p=0.149).

The frequency of occurrence pairwise tests showed a graded response: monocotyledonous plants occurred significantly the most, followed by dicotyledonous plants and other unidentifiable contents equally and lastly unidentifiable vertebrate remains (Figure 27) (Table 12).

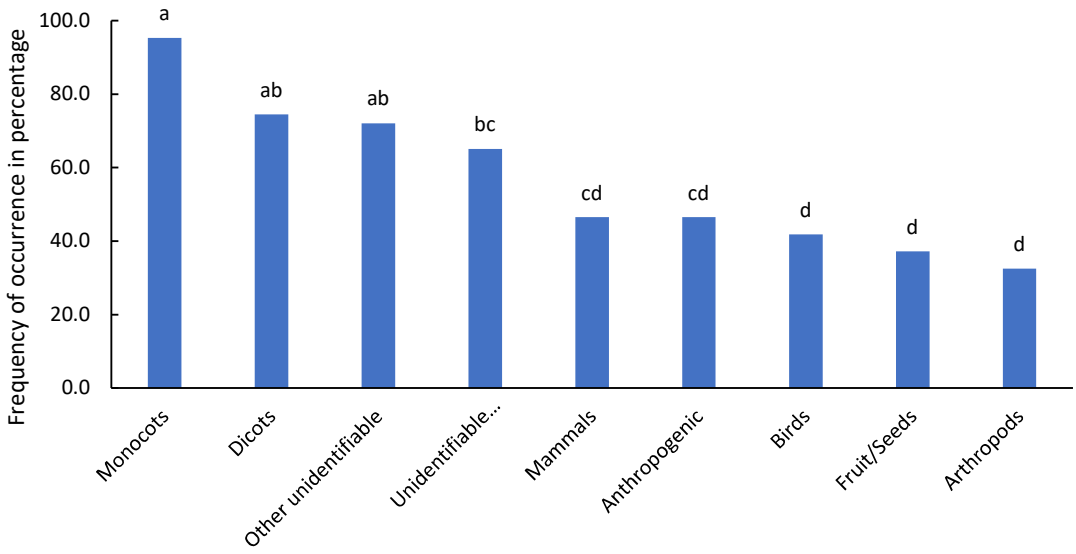


Figure 27. The frequency of occurrence of each component in the scat of black-backed jackals during winter at the Jackal Creek Golf Estate. The components are arranged from highest to lowest for ease of comparison. Bars with different letters indicate significant differences.

Table 12. Pairwise chi-squared comparisons of the frequency of occurrence scat components of black-backed jackals at the Jackal Creek Golf Estate in winter 2019. Df=1 for all tests. Significant comparisons are shown in bold.

Comparison	χ^2 value	p-value
Anthropogenic vs. Mammals	0.00	1.000
Anthropogenic vs. Birds	0.24	0.621
Anthropogenic vs. Arthropods	2.46	0.117
Anthropogenic vs. Unidentifiable vertebrates	3.10	0.078
Anthropogenic vs. Monocots	**16.81**	**<0.001**
Anthropogenic vs. Dicots	**6.44**	**0.011**
Anthropogenic vs. Fruits/seeds	1.03	0.309
Anthropogenic vs. Other	**5.52**	**0.019**
Mammals vs. Birds	0.24	0.621
Mammals vs. Arthropods	2.46	0.117
Mammals vs. Unidentifiable vertebrates	3.10	0.078
Mammals vs. Monocots	**16.81**	**<0.001**
Mammals vs. Dicots	**6.44**	**0.011**
Mammals vs. Fruits/seeds	1.03	0.309
Mammals vs. Other	**5.52**	**0.019**
Birds vs. Arthropods	1.16	0.281
Birds vs. Unidentifiable vertebrates	**5.06**	**0.025**
Birds vs. Monocots	**20.85**	**<0.001**

Birds vs. Dicots	**9.12**	**0.003**
Birds vs. Fruits/seeds	0.27	0.601
Birds vs. Other	**8.02**	**0.005**
Arthropods vs. Unidentifiable vertebrates	**10.85**	**0.001**
Arthropods vs. Monocots	**30.82**	**<0.001**
Arthropods vs. Dicots	**16.38**	**<0.001**
Arthropods vs. Fruits/seeds	0.31	0.578
Arthropods vs. Other	**14.94**	**<0.001**
Unidentifiable vertebrates vs. Monocots	**5.70**	**0.017**
Unidentifiable vertebrates vs. Dicots	0.62	0.431
Unidentifiable vertebrates vs. Fruits/seeds	**7.61**	**0.006**
Unidentifiable vertebrates vs. Other	0.35	0.551
Monocots vs. Dicots	2.58	0.108
Monocots vs. Fruits/seeds	**25.50**	**<0.001**
Monocots vs. Other	3.23	0.072
Dicots vs. Fruits/seeds	**12.40**	**<0.001**
Dicots vs. Other	0.04	0.848
Fruits/seeds vs. Other	**11.13**	**0.001**

For the percentage mass contribution, pairwise tests showed that unidentifiable vertebrate remains occurred significantly more often (Figure 28) than arthropods, dicotyledonous plants, fruits and seeds and other unidentifiable contents (Table 13).

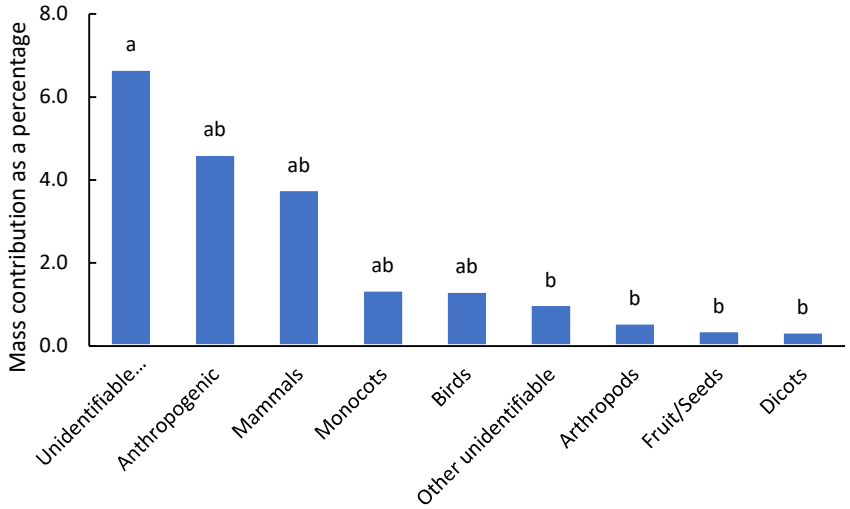


Figure 28. The percentage mass contribution of each component in the scat of the black-backed jackal during winter at the Jackal Creek Golf Estate. The components are arranged from highest to lowest for ease of comparison. Bars with different letters indicate significant differences.

Table 13. Pairwise chi-squared comparisons of percentage mass contribution of scat components of black-backed jackals at the Jackal Creek Golf Estate in winter 2019. Df=1 for all tests. Significant comparisons are shown in bold.

Comparison	χ^2 value	p-value
Anthropogenic vs. Mammals	0.09	0.770
Anthropogenic vs. Birds	1.83	0.176
Anthropogenic vs. Arthropods	3.18	0.074
Anthropogenic vs. Unidentifiable vertebrates	0.37	0.542
Anthropogenic vs. Monocots	1.79	0.181
Anthropogenic vs. Dicots	3.68	0.055
Anthropogenic vs. Fruits/seeds	3.60	0.058
Anthropogenic vs. Other	2.32	0.128
Mammals vs. Birds	1.18	0.278
Mammals vs. Arthropods	2.38	0.123
Mammals vs. Unidentifiable vertebrates	0.80	0.370
Mammals vs. Monocots	1.14	0.285
Mammals vs. Dicots	2.85	0.091
Mammals vs. Fruits/seeds	2.78	0.095
Mammals vs. Other	1.60	0.206
Birds vs. Arthropods	0.31	0.578
Birds vs. Unidentifiable vertebrates	3.58	0.059
Birds vs. Monocots	0.00	0.987
Birds vs. Dicots	0.58	0.448
Birds vs. Fruits/seeds	0.53	0.467
Birds vs. Other	0.04	0.835
Arthropods vs. Unidentifiable vertebrates	**5.17**	**0.023**
Arthropods vs. Monocots	0.33	0.567
Arthropods vs. Dicots	0.05	0.821
Arthropods vs. Fruits/seeds	0.04	0.850
Arthropods vs. Other	0.13	0.721
Unidentifiable vertebrates vs. Monocots	3.53	0.060
Unidentifiable vertebrates vs. Dicots	**5.71**	**0.017**
Unidentifiable vertebrates vs. Fruits/seeds	**5.62**	**0.018**
Unidentifiable vertebrates vs. Other	**4.18**	**0.041**
Monocots vs. Dicots	0.60	0.440
Monocots vs. Fruits/seeds	0.55	0.459
Monocots vs. Other	0.05	0.823
Dicots vs. Fruits/seeds	0.00	0.970
Dicots vs. Other	0.32	0.569
Fruits/seeds vs. Other	0.29	0.592

The numerical frequency of scat components is shown in Figure 29.

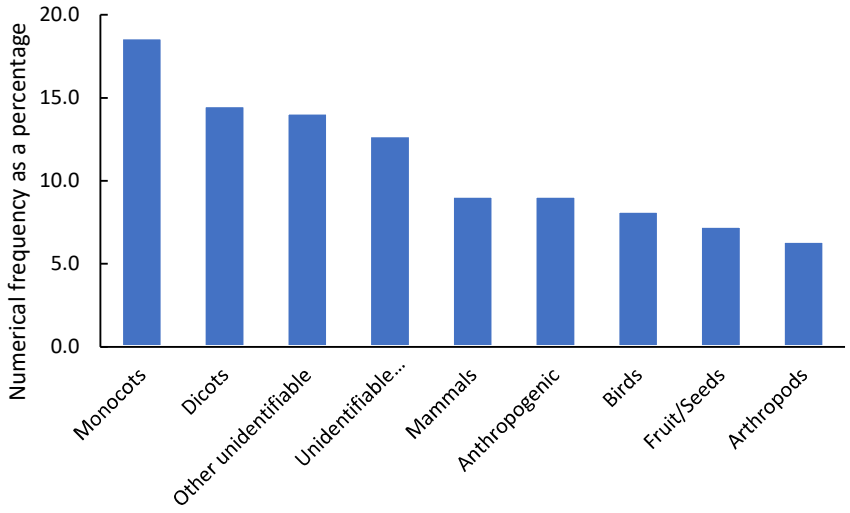


Figure 29. The numerical frequency of occurrence of components in the scats of black-backed jackals during winter at the Jackal Creek Golf Estate. The components are arranged from highest to lowest for ease of comparison. There was no significant difference between the components.

Summer samples

In summer, monocotyledonous plants occurred most frequently in scats, followed by unidentifiable vertebrate matter, occurring in 85.2% and 70.4% of scats, respectively. The least frequently occurring components in summer were mammals, fruits and seeds, and other unidentifiable matter, all occurring in 37.0% of scats. The frequency of occurrence of the various components in summer differed significantly from chance (χ^2=42.59; df=8; p<0.001). For the percentage mass contribution, the occurrence of the various scat components in summer also differed significantly from chance (χ^2=49.81; df=8; p<0.001). However, the numerical frequency of the various scat components did not differ significantly from chance (χ^2=8.98; df=8; p=0.344).

The frequency of occurrence pairwise tests for summer scat components also showed a graded response: monocotyledonous plants occurred significantly the most, followed by unidentifiable vertebrate remains and lastly arthropods (Figure 30) (Table 14).

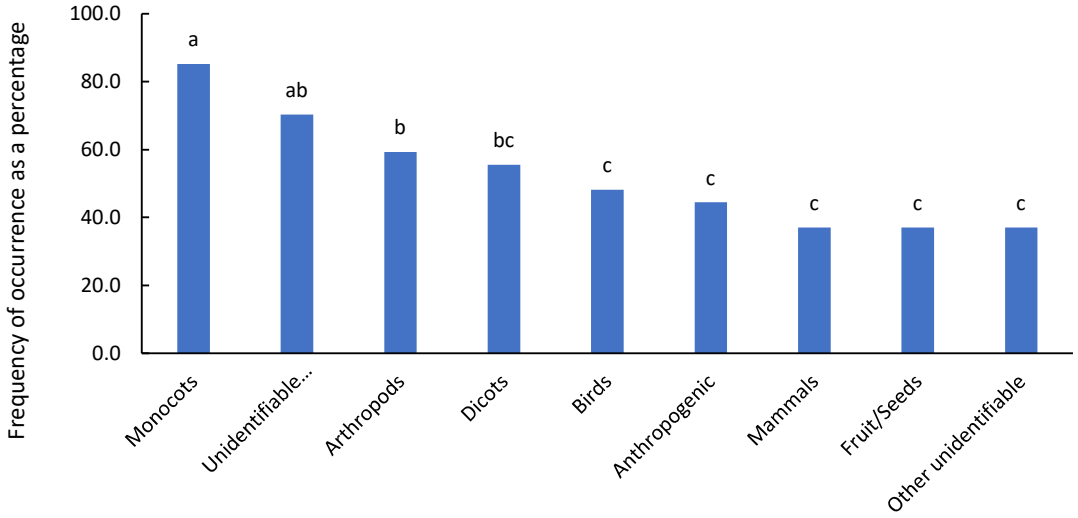


Figure 30. The frequency of occurrence of scat components of the black-backed jackals during summer at the Jackal Creek Golf Estate. The components are arranged from highest to lowest for ease of comparison. Bars with different letters indicate significant differences.

Table 14. Pairwise chi-squared comparisons of the frequency of occurrence scat components of black-backed jackals at the Jackal Creek Golf Estate in summer 2019/2020. Df=1 for all tests. Significant comparisons are shown in bold.

Comparison	χ^2 value	p-value
Anthropogenic vs. Mammals	0.67	0.412
Anthropogenic vs. Birds	0.15	0.700
Anthropogenic vs. Arthropods	2.12	0.146
Anthropogenic vs. Unidentifiable vertebrates	**5.85**	**0.016**
Anthropogenic vs. Monocots	**21.35**	**<0.001**
Anthropogenic vs. Dicots	1.23	0.267
Anthropogenic vs. Fruits/seeds	0.67	0.412
Anthropogenic vs. Other	0.67	0.412
Mammals vs. Birds	1.45	0.229
Mammals vs. Arthropods	**5.13**	**0.024**
Mammals vs. Unidentifiable vertebrates	**10.34**	**0.001**
Mammals vs. Monocots	**18.97**	**<0.001**
Mammals vs. Dicots	3.70	0.054
Mammals vs. Fruits/seeds	0.00	1.000
Mammals vs. Other	0.00	1.000
Birds vs. Arthropods	**16.11**	**<0.001**
Birds vs. Unidentifiable vertebrates	**4.17**	**0.041**
Birds vs. Monocots	**10.29**	**0.001**
Birds vs. Dicots	0.53	0.467
Birds vs. Fruits/seeds	1.45	0.229

Birds vs. Other	1.45	0.229
Arthropods vs. Unidentifiable vertebrates	0.95	0.329
Arthropods vs. Monocots	**4.65**	**0.031**
Arthropods vs. Dicots	0.12	0.730
Arthropods vs. Fruits/seeds	**5.13**	**0.024**
Arthropods vs. Other	**5.13**	**0.024**
Unidentifiable vertebrates vs. Monocots	1.41	0.235
Unidentifiable vertebrates vs. Dicots	1.74	0.187
Unidentifiable vertebrates vs. Fruits/seeds	**10.34**	**0.001**
Unidentifiable vertebrates vs. Other	**10.34**	**0.001**
Monocots vs. Dicots	**6.24**	**0.013**
Monocots vs. Fruits/seeds	**18.97**	**<0.001**
Monocots vs. Other	**18.97**	**<0.001**
Dicots vs. Fruits/seeds	3.70	0.054
Dicots vs. Other	3.70	0.054
Fruits/seeds vs. Other	0.00	1.000

For the percentage mass contribution, pairwise tests showed that unidentifiable vertebrate remains occurred significantly more often (Figure 31) than anthropogenic matter, mammals, birds, arthropods, monocotyledonous plants, dicotyledonous plants, fruits and seeds and other unidentifiable contents (Table 15).

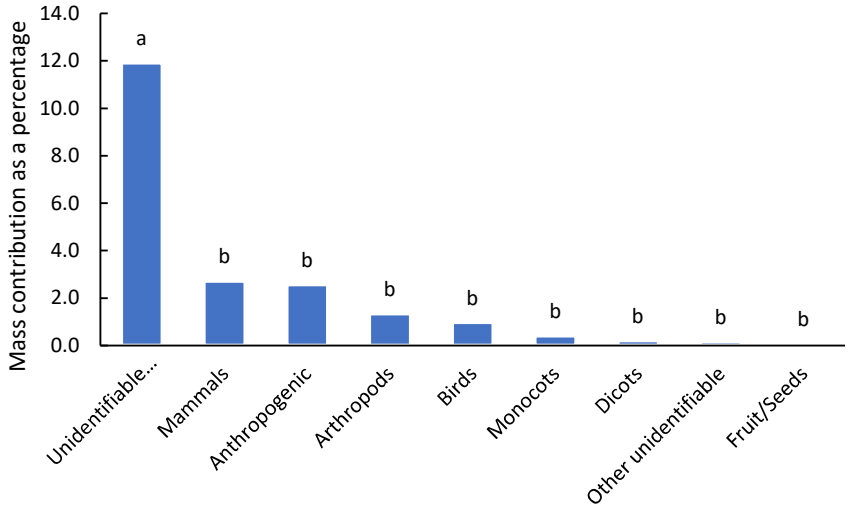


Figure 31. The percentage mass contribution of each scat component of the black-backed jackal during summer at the Jackal Creek Golf Estate, South Africa. The components are arranged from highest to lowest for ease of comparison. Bars with different letters indicate significant differences.

Table 15. Pairwise chi-squared comparisons of percentage mass contribution of scat components of black-backed jackals at the Jackal Creek Golf Estate in summer 2019/2020. Df=1 for all tests. Significant comparisons are shown in bold.

Comparison	χ^2 value	p-value
Anthropogenic vs. Mammals	0.00	0.949
Anthropogenic vs. Birds	0.72	0.397
Anthropogenic vs. Arthropods	0.38	0.535
Anthropogenic vs. Unidentifiable vertebrates	**6.03**	**0.014**
Anthropogenic vs. Monocots	1.56	0.210
Anthropogenic vs. Dicots	2.00	0.157
Anthropogenic vs. Fruits/seeds	2.37	0.124
Anthropogenic vs. Other	2.09	0.149
Mammals vs. Birds	0.82	0.364
Mammals vs. Arthropods	0.47	0.495
Mammals vs. Unidentifiable vertebrates	**5.79**	**0.016**
Mammals vs. Monocots	1.71	0.191
Mammals vs. Dicots	2.14	0.143
Mammals vs. Fruits/seeds	2.52	0.113
Mammals vs. Other	2.23	0.135
Birds vs. Arthropods	0.06	0.809
Birds vs. Unidentifiable vertebrates	**9.29**	**0.002**
Birds vs. Monocots	0.23	0.630
Birds vs. Dicots	0.49	0.484
Birds vs. Fruits/seeds	0.78	0.376
Birds vs. Other	0.55	0.457
Arthropods vs. Unidentifiable vertebrates	**8.44**	**0.004**
Arthropods vs. Monocots	0.50	0.480
Arthropods vs. Dicots	0.82	0.364
Arthropods vs. Fruits/seeds	1.15	0.284
Arthropods vs. Other	0.90	0.344
Unidentifiable vertebrates vs. Monocots	**10.75**	**0.001**
Unidentifiable vertebrates vs. Dicots	**11.30**	**0.001**
Unidentifiable vertebrates vs. Fruits/seeds	**11.72**	**0.001**
Unidentifiable vertebrates vs. Other	**11.41**	**0.001**
Monocots vs. Dicots	0.06	0.803
Monocots vs. Fruits/seeds	0.24	0.625
Monocots vs. Other	0.09	0.763
Dicots vs. Fruits/seeds	0.07	0.790
Dicots vs. Other	0.00	0.955
Fruits/seeds vs. Other	0.05	0.830

The numerical frequency of scat components is shown in Figure 32.

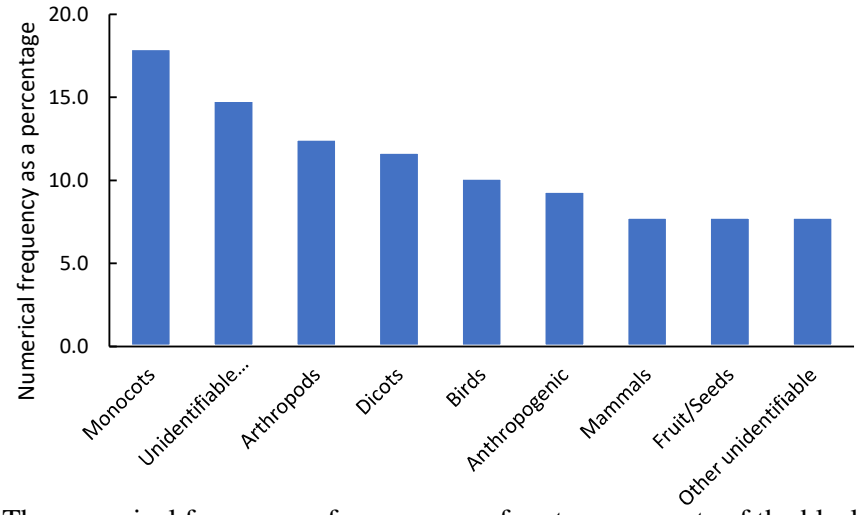


Figure 32. The numerical frequency of occurrence of scat components of the black-backed jackal during summer at the Jackal Creek Golf Estate. The components are arranged from highest to lowest for ease of comparison. There was no significant difference between the components.

DISCUSSION

My study had two aims. The first aim was to establish the occurrence of black-backed jackals in Greater Johannesburg, to ascertain the prevalence of the species in urban Johannesburg. The second aim was to assess the mechanisms that allow black-backed jackals to live in urban areas, by focussing on the population occurring at Jackal Creek Golf Estate.

I had four objectives: 1) to establish the current black-backed jackal areas of occurrence and absence in Greater Johannesburg, using sightings reported by members of the public via social media; 2) to examine the activity patterns of the black-backed jackals within the Estate, particularly the general daily activity profile and seasonal variation in activity; 3) to assess the temporal and spatial patterns of behaviour of the black-backed jackals within the Estate and 4) to establish the diet of the black-backed jackal population at the Estate through scat analysis. The findings of each of these objectives are discussed below.

Species Distribution

Studies thus far about the distribution of black-backed jackals have focussed mainly on their general distribution in Africa rather than their more specific distribution in South Africa. The literature mentions that their distribution in South Africa is widespread, generally coinciding with the availability of food resources (Loveridge and Nel, 2004). Previous studies mentioned that black-backed jackals utilise human habitation as a result of the abundance of resources it may provide (Loveridge and MacDonald, 2003). Here, I investigated the specific urban distribution of black-backed jackals in the Greater Johannesburg area, in order to assess their occurrence in urban areas.

From my survey of the public on social media platforms, it appeared that most occurrences of black-backed jackals were in the northern parts of Johannesburg. All sightings that were reported by the public were in areas currently undergoing urban development and bordering on more natural areas suitable for black-backed jackals. These natural areas included the Modderfontein Nature Reserve and agricultural small holdings of Bredell on the Eastrand, the river course of the Jukskei near Dainfern in the North, and Muldersdrift in the West. Reports may also have occurred in the northern parts of the designated area due to the southern areas being more developed and potentially unsuitable for black-backed jackals. Perhaps if the designated area (which comprised of any sightings within a 30km radius from

the Johannesburg CBD) (Figure 3), extended to the edge of these developed areas in the south, more sightings might have been reported.

More meaningful conclusions could not be drawn as a result of the low number of responses to the survey. This low response could be due to a lack of sightings, with black-backed jackals occurring very rarely in peri-urban and urban centres because of high human density and built-up areas. Different carnivore species show different responses with regard to high human density and level of urban development (Ordenana et al., 2010). In Wroclaw, Poland, stone martens show a preference for urban centres, whereas red foxes favour underdeveloped areas closer to urban-rural interfaces where human population density is low (Dudus et al., 2014). Alternatively, a lack of access of the human residents to online platforms such as Facebook or a lack of knowledge or confusion about the identity of black-backed jackals (i.e. they were assumed to be domestic dogs) could have resulted in a poor response rate to the survey. One of the challenges that arises with citizen-based science is data inaccuracy (Conrad and Hilchey, 2011), particularly with regard to the identification of species (Aceves-Bueno et al., 2017). For example, the actual abundance of the exotic lady beetle (*Harmonia axyridis*) in the British Isles through a citizen science project was underreported due to misidentification of *H. axyridis* by citizen scientists (Gardiner et al., 2012).

Activity patterns

In many parts of their natural distributional range, black-backed jackals display a bimodal peak in activity, an evening crepuscular peak and a nocturnal peak (Rowe-Rowe, 1983; Ferguson *et al*., 1988; Hiscocks and Perrin, 1988). Exceptions to this have been noted in cases where the jackals have access to a year-round, abundant food supply, such as in the Cape Cross Seal Reserve in Namibia, where black-backed jackals were active during the day throughout the year (Hiscocks and Perrin, 1988). Black-backed jackals in natural areas increase their number of hours of activity in winter compared to summer, which is suggested to be as a result of a difference in the times of sunrise and sunset, as well as temperature fluctuations between winter and summer, and the general breeding biology of black-backed jackals (Kaunda, 2000). Here, I assessed whether the daily and seasonal activity profile of the black-backed jackals residing at Jackal Creek Golf Estate is similar to the activity patterns of black-backed jackals in natural areas.

Winter

As predicted, the daily activity profile of the black-backed jackals at the Estate in winter presented a bimodal peak with an evening crepuscular peak and a nocturnal peak, resembling the daily activity pattern of black-backed jackal in natural areas (Ferguson et al., 1988; Kaunda, 2000). Some instances of unusual activity occurred in winter. The reasons for these included cameras possibly being placed along part of a thoroughfare which the black-backed jackals used to travel to other areas where different activities were carried out (i.e. Sites 7 and 25). One site showed a peak in activity in the morning and afternoon, with little to no activity in the evening and nocturnally (Site 18), which was possibly because of the camera being placed at a resting site; resting in the morning and afternoon is typical of naturally-occurring black-backed jackals (Ferguson *et al*., 1988; Kaunda, 2000). In some instances, abnormal, excessively high peaks in activity were recorded due to few videos of black-backed jackals being captured at these sites (Site 27) which is registered as high density at a particular time in the R 'densityplot' function.

Summer

The typical daily activity profile of naturally-occurring black-backed jackal showed an evening crepuscular peak and a nocturnal peak (Rowe-Rowe, 1983). In contrast, the activity pattern of the black-backed jackals at the Estate in summer showed two peaks, an extended evening crepuscular peak and a nocturnal peak, which differed from my prediction of a typical bimodal peak. This increased occurrence of nocturnal activity is unusual. There are at least four non-mutually exclusive reasons for the change in activity profile of the black-backed jackals. First, the change in activity profile may indicate that the black-backed jackals altered their behaviour in urban areas. Urban exploiters are wildlife that change their behaviour in the presence of humans, as occurs in dingoes (*Canis lupus dingo*) and coyotes (*Canis latrans*). These predators adjust their activity patterns to avoid humans. For example, coyotes become more active at night to avoid human activity during the day (Gehrt, 2007) and dingoes restrict their movement to times of reduced human activity to avoid hazards such as road traffic (Allen et al., 2013). Similarly, the black-backed jackals at the Estate appear to be utilising the Estate at night when human activity is reduced. Second, in summer, there was an increase in human activity on the golf course at the Estate during the day, starting at sunrise, and it is possible that the reduced activity by black-backed jackals during the day coincided with increased human activity. Third, naturally-occurring black-backed jackals also

display a reduction in diurnal activity during higher daytime temperatures (Kaunda, 2000), most likely to reduce thermoregulation costs. Canids have been documented to reduce activity during periods of high temperatures by the timing of their activity periods during periods of lower temperature, such as in kit foxes (*Vulpes macrotis*) (Golightly and Ohmart, 1983). Fourth, the black-backed jackals at the Estate may be adjusting their activity time to coincide with that of their prey (Kaunda, 2000, 2001) which being at an urban estate may comprise of synanthropic rodents such as black rats (*Rattus rattus*) and house mice (*Mus musculus*), which are usually nocturnal (Bjornson and Wright, 1960; Recht, 1988).

Again, some instances of unusual activity were noted during the season. Although the overall daily summer activity pattern showed two peaks, some sites (Site 1.1 and 7), displayed a single activity peak at either dusk or dawn similar to naturally-occurring black-backed jackals which show a peak at dusk and dawn (Rowe-Rowe, 1983; Ferguson *et al*., 1988; Hiscocks and Perrin, 1988). At some sites (Sites 3 and 33), the predominant behaviour was travel, suggesting that the camera placement was along a thoroughfare for the black-backed jackals. Again, in some instances, excessively high peaks in activity were recorded due to few videos being captured at sites (i.e. Site 16) which are registered as high density at a particular time by the R 'densityplot' function.

Winter vs. summer

The comparison of activity patterns in winter and summer showed very little seasonal difference overall, which is in support of my prediction. There was a 1-hour difference in peak activity times between winter and summer, with the winter peaks occurring an hour earlier than the summer peaks. This 1-hour difference is most likely due to the change in daylight hours from winter to summer, with sunset occurring earlier in winter, and represents the seasonal changes in daylight hours at the geographic location of the study site. This coincided with the earlier crepuscular peak in activity in winter compared to summer. The change in daylight hours and warmer temperatures would also account for the lower activity in the afternoon in summer compared to winter, which also occurs in naturally-occurring black-backed jackals (Kaunda, 2000). The cooler weather in winter also results in the reduction of activity of humans at the Estate, permitting the jackals to exploit more areas of the Estate and be active at the times noted in naturally occurring black-backed jackals.

Behaviour

Here, I studied the behaviour of the black-backed jackals at the Estate to ascertain whether they displayed certain behaviours more often than others and whether they displayed temporal and spatial variation of behaviours. Naturally-occurring black-backed jackals show temporal distribution of behaviours, resting predominantly during the day while hunting/foraging at night which is presumed to correspond with the activity times of their prey (Kaunda, 2000). Nattrass et al. (2017) found that black-backed jackals change their behaviour spatially as a consequence of local environmental conditions, such as food availability, human persecution, and the presence or absence of competitive species. This is seen in the Cape Cross Seal Reserve where territorial behaviours are displayed outside of the seal colony, whilst more tolerance is shown when foraging at the seal colony (Jenner et al., 2011).

Kaunda (2000) studied the seasonal and diel activity of black-backed jackals in Mokolodi Nature Reserve in Botswana, and as far as I am aware is the only comprehensive study of the behavioural ecology of naturally occurring jackals. He assigned activity into four time brackets and found that hunting/foraging was the most commonly observed activity, followed by travel/locomotion, whereas resting and social interactions were recorded least. The majority of the different behavioural types (e.g. hunting/foraging, locomotion/travel, flight, resting and social interactions) were recorded from early evening, overnight until mid-morning. Most consistent with my study was the prevalence of hunting/foraging activity in the early evenings, resting which was recorded as a common diurnal activity, and travel/locomotion being predominant during crepuscular and nocturnal hours (Kaunda, 2000). This presumably represents the pattern of activity types seen in most naturally occurring black-backed jackals. The only noticeable differences in the occurrence of behavioural types recorded between seasons in Mokolodi Nature Reserve was an increase in flight (human avoidance behaviour) and social interactions in winter compared to summer (Kaunda, 2000).

Behaviours by time period

Like naturally occurring black-backed jackals (Kaunda, 2000), most activity of the jackals at the Estate was recorded in the early evening, through to mid-morning, with rest being recorded during the day. Social interactions, including affiliative, play and aggression were recorded more often in winter, which is typical of black-backed jackals during their mating season (Ferguson et al., 1988; Kaunda, 2000; Jenner et al., 2011) from June and

continuing into July in southern Africa (Ferguson et al., 1983; McKenzie, 1993; Nattrass et al., 2017).

In support of my predictions, the behaviour of the black-backed jackals at the Estate varied daily. Resting occurred predominantly during the day, while foraging was recorded in minimal levels and was distributed throughout the 24 h of the day at different times. Travel and rest were the most frequently recorded behaviours of the black-backed jackals in both winter and summer. This differed from the hunting/foraging behaviour recorded most frequently in naturally occurring black-backed jackals (Kaunda, 2000), possibly as a result of the human presence at the Estate compared to that of Mokolodi Nature Reserve. This reduction in hunting/foraging behaviour in the black-backed jackals at the Estate may also be a result of easily available anthropogenic food. Temporally, the black-backed jackals at the Estate differed in behaviour in winter compared with summer. The greater occurrence of travel in winter compared with summer, as also observed in naturally occurring black-backed jackals, may be as a result of a reduction of resources in winter, causing the jackal to search more for food (Rowe-Rowe, 1983). Travel and rest both occurred significantly more frequently in winter from evening throughout the night compared to summer. However, most travel and rest in summer also occurred during this time, just to a lower extent than recorded in winter. The high levels of travel recorded nocturnally differs from the behaviour seen in naturally occurring black-backed jackals, whose movement is largely influenced by time of day: naturally occurring black-backed jackals travelled greater distances during dawn and twilight (Kaunda, 2001).

Behaviours by location

As predicted, the black-backed jackals displayed different behaviours more often in some areas of the Estate than others. In winter, travel occurred in all areas of the Estate whereas the other six behaviours occurred most often in the western parts of the Estate. Differences in the variety of behaviours in different parts of the Estate may be as a result of the locations of the den sites here; more behaviours occurred closer to denning sites with travel occurring in areas between dens. The exact location of the den sites at the Estate would need to be determined to further confirm this assumption. The western part of the Estate was also where most aggression was recorded between the black-backed jackals, suggesting territorial behaviours, assuming that these were between breeding groups. Territories of black-backed jackal breeding pairs are generally defended indirectly via scent-marking and

the use of faeces as visual markers (McKenzie, 1993; Kaunda, 1998; Loveridge and Nel, 2004), and with core territories which incorporate den sites being defended directly through aggressive interactions (McKenzie, 1993; Kaunda, 1998; Jenner et al., 2011). The eastern part of the Estate comprised of a greater portion of the human residences, so in order to avoid human contact, the jackals may have displayed more travelling compared to other behavioural types in this area. Many carnivores in urban environments avoid humans (Patten et al., 2019). For example, brown bears (*Ursus arctos*) in Fennoscandia, Finland avoid urban areas (Moen et al., 2019), and even small to medium-sized carnivores, such as stone martens (*Martes foina*) in Luxembourg shift their activity patterns to times of lowest human activity (Herr, 2008) and coyotes which avoid areas of higher development in urban environments (Moll et al., 2018). Coyotes have even been documented to increase their travelling speed to move through highly developed urban areas more rapidly (Mueller et al., 2018). This may be the same pattern as seen in the black-backed jackals at the Estate in my study.

In summer, travel was displayed in all the zones, with the majority of the occurrences being recorded in the northern parts of the Estate and minimal occurrences of other behavioural types were recorded. The north-western parts of the Estate were within the undeveloped corridor mentioned above, while the north-eastern border of the Estate was undergoing development during my study (pers obs.), both of which may have provided opportunities for the jackals to leave the Estate into green corridors that connect the Estate to more natural areas. Some urban animals adjust their behaviour spatially, such as striped field mice (*Apodemus agrarius*) which show greater spatial exploration in urban areas (Dammhahn et al., 2020). The lack of the other six behaviour types and lower number of occurrences of black-backed jackals recorded in summer footage may be related to the increased activity of humans at the Estate in summer, particularly the activity of golfers and golf course personnel (Bennet pers comm.).

Diet

In natural areas, black-backed jackal diets comprise of mammalian species predominantly, and can also include other components, such as fruits, insects and other invertebrates, birds and reptiles (du P Bothma, 1971; Kaunda and Skinner, 2003). Canids show variation with regard to their diet, often consuming foods that are in abundance in their habitat (MacDonald and Sillero-Zubiri, 2004), which also applies to black-backed jackals. Studies have shown that black-backed jackals may select food resources according to their

energy demands, selecting foods with higher nutritional value, such as small mammals due to their higher protein content (Kaunda and Skinner, 2003), a behaviour observed in coyotes (Harrison and Harrison, 1984). Klare et al. (2010) and Kaunda and Skinner (2003) also suggest that when protein requirements of black-backed jackals are lower, they may shift their diet to more easily acquired carbohydrates, such as fruits.

Here, I assessed the diet of the black-backed jackals at the Estate seasonally and also studied whether their diet contained a sizable portion of anthropogenic food as a result of their proximity to humans. As predicted, the indices calculated in this study, Simpson's diversity index and Levin's standardised index, both indicated a large degree of diversity in the diet and thus a generalist diet for the black-backed jackals at the Estate. Diversity indices are used as a metric assessment of diet breadth. The high diversity indicated by the Simpson's diversity index of 0.88 in my study concurs with the index of 0.86 in naturally occurring black-backed jackals (Klare et al. 2010), whose diets are varied and change according to the seasonal availability of resources (du P Bothma, 1971; Kaunda and Skinner, 2003; Klare et al., 2010). However, the non-urban study by Klare et al. (2010) indicated a lower Levin's standardised index and thus diet breadth (0.21) in black-backed jackal than the index of 0.91 calculated in my study, also aligning with my predictions that stated that the diet breadth of the jackals at the Estate would be wider than that of naturally occurring black-backed jackal. This may be as a result of the incorporation of anthropogenic items in the diet of the black-backed jackals at the Estate.

The frequency of occurrence of scat components differed seasonally, with arthropods being consumed significantly more often in summer than winter, and other unidentifiable components occurring significantly more often in winter than summer. The Estate occurs in a summer rainfall region, and arthropods, notably insects, are recorded more often in the wet seasons (Wolda, 1988), which could explain the greater occurrence in the jackals' diet in summer compared with winter. Other unidentifiable components ranked third in winter and seventh in summer. The higher occurrence of unidentifiable components in winter was possibly due to a reduction of resources in winter, and the black-backed jackals consuming the most readily available foods (Rowe-Rowe, 1983; Atkinson et al., 2002), such as scraps found in dustbins around the Estate, which only left unidentifiable traces in the scat.

In both seasons, the GPS locations of the collected scat samples showed a clustering of samples in the North and South of the Estate. Scat containing anthropogenic matter was located neither particularly close to nor far away from the human residences. Although I sampled the Estate extensively on foot for scat, my sampling was opportunistic, which might

explain the clustering of scats in my study. Black-backed jackals use faeces to mark territorial borders (McKenzie, 1993; Loveridge and Nel, 2004), often defecating on prominent objects like rocks or grass tufts alongside pathways and roads (Humphries *et al*., 2015). This use of scat as territorial markers may have resulted in my sampling in areas where the jackals at the Estate occur, leading to clustering of scat samples collected. Further studies may need to systematically sample for scat in order to better ascertain a pattern of defaecation of the jackals at the Estate.

In winter, monocotyledonous material followed by dicotyledonous matter ranked as the highest scat components of the black-backed jackals according to the frequency of occurrence. Similarly, for summer, the highest-ranked component of the scat was monocotyledonous plants. This differs from the diet components of naturally occurring black-backed jackals. Through scat analysis, small mammals were determined to be the main component of black-backed jackal diet in Giant's Castle Game Reserve in KwaZulu-Natal, South Africa (Rowe-Rowe; 1983) and Mokolodi Nature Reserve, Botswana (Kaunda and Skinner, 2003), comprising 56% and 32.4% of the diet, respectively. Thus, it appears that plant matter is not a usual component of the black-backed jackal diet, but the abundance of grass on the golf course may result in incidental ingestion by black-backed jackals at the Estate when consuming other food items, as also suggested for naturally occurring black-backed jackal (Grafton, 1965; Rowe-Rowe, 1983). However, the particularly large quantity of grass in the scats in my study is similar to that of domestic canids which deliberately ingest grass for fibre requirements (Kang et al., 2007). Thus, it might be that the black-backed jackals at the Estate deliberately consume grass, which has also been noted occasionally in naturally occurring black-backed jackals, presumably for roughage (Grafton, 1965; du P Bothma, 1971; Rowe-Rowe, 1983).

Unidentifiable vertebrates were the next most frequent components in scats in winter (fourth) and ranked as the second-highest component in summer. The unidentifiable vertebrate remains comprised predominantly of fragments of bones, as well as larger pieces of bone that could not be from naturally occurring rodents or birds, or any presumed natural prey within the area. It is possible that these were shards of lamb bones (*Ovis aries*) or chicken bones (*Gallus gallus domesticus*). There were no sources of these larger mammalian prey animals identified in the direct vicinity of the Estate (pers obs.). Thus, it is presumed that these would be acquired by the jackal scavenging through dustbins or bones being left out for them by human residents at the Estate. However, with the jackals being able to leave the Estate, there is the possibility that these unidentified vertebrate remains have been

acquired outside of the confines of the Estate. If these bones are identified to species and linked directly to anthropogenic sources, these would constitute part of the anthropogenic components of the diet. Since this level of identification was not done, it would suggest that the number of anthropogenic items in the diet is underrepresented in my study. Residents barbecuing at the Estate are regularly visited by the jackals (Bennet pers comm.). This could result in residents throwing bones out to the jackals more readily, despite the heavy fines imposed if they are caught feeding the jackals. South Africans are known to barbecue more often in summer because of the better weather which could explain the greater occurrence of unidentifiable vertebrates in the jackals' diet in summer. The jackals at the Estate have also been reported to attack domestic pets (Bennet pers comm.), as well as stray cats (*Felis catus*) (Weil, 2017). These may also constitute a part of the unidentifiable vertebrate remains found in the scat samples.

Mammal remains and anthropogenic components occurred in equal amounts in the scat samples in winter. Mammal remains comprised predominantly of naturally occurring rodents, mostly southern African vlei rats (*Otomys irroratus*). This composition of naturally occurring rodents in the diet is similar to the diet of naturally occurring black-backed jackals (Grafton, 1965; du P Bothma, 1971; Rowe-Rowe, 1983; Kaunda and Skinner, 2003). Aligning with my predictions, anthropogenic foods comprised 46.5% and 44.4% in winter and summer, respectively; I predicted that anthropogenic food would be among the main components of the black-backed jackals' diet at the Estate based on the percentage occurrence in scats. The frequency of occurrence of anthropogenic food in diet varies by species and geographic region. Anthropogenic foods comprise 83.5% of the diets of urban foxes (*Vulpes vulpes*) in Zurich, Switzerland had 83.5% (Contesse et al., 2004). The occurrence of anthropogenic foods in coyotes ranged from 24% in metropolitan areas of the United States (Gehrt, 2007) to 30% in Alberta, Canada (Murray et al., 2015b). In dingoes on Fraser Island, Australia, human-sourced food comprised 7.5-46.9% of their diet (Behrendorff et al., 2016). However, due to the possible underrepresentation of anthropogenic foods in the scat, my results must be interpreted with caution.

Anthropogenic materials in the black-backed jackal scat in my study included items, such as balloons, pieces of serviettes, glass, and fabric. These items have no apparent nutritional value and are probably ingested incidentally when consuming food items scavenged from bins. Due to the highly digestible nature of many anthropogenic foods (Oste, 1991; Kiers et al., 2000; Allen et al., 2016), for example, bread, the amount of anthropogenic matter may be further underrepresented (Hewitt and Robbins, 1996; Allen et al., 2016). This

incorporation of anthropogenic foods into the diet may be beneficial to the black-backed jackals at the Estate since these foods are more readily available (Contesse et al., 2004; McKinney, 2006), especially in winter when there is lower availability of natural food sources (Luniak, 2004; Murray et al., 2015a). Even in naturally occurring black-backed jackals in the Mokolodi Nature Reserve in Botswana, anthropogenic items were more common diet components in winter (26.4%) than summer (6%) (Kaunda and Skinner, 2003). This reserve is situated approximately 15km from the country's capital of Gaborone. Coyotes in southern California display a similar seasonal diet variation, with anthropogenic foods making up 11-13% of their diet in the dry season, and 3-5% in the wet season (Fedriani et al., 2001).

Bird remains ranked fifth in summer, compared with sixth in winter. Other studies of black-backed jackal diet indicate a low consumption of birds (Grafton, 1965; du P Bothma, 1971; Rowe-Rowe, 1983; Kaunda and Skinner, 2003), which is probably due to the comparatively low success rate of canids catching birds (Reynolds and Aebischer, 1991; Lovari and Parigi, 1995). However, the abundance of ground-dwelling summer hatchlings, such as helmeted guinea fowl (*Numida meleagris*) and Egyptian geese (*Alopochen aegyptiaca*) (Ratcliffe and Crowe, 2001) at the Estate (pers obs.), may account for the higher occurrence of birds in the scat in summer.

All other scat components, fruits and seeds and arthropods, occurred in minimal levels in winter. The low occurrence of fruits and seeds in the scat is most likely as a result of the low availability of these items during winter as also seen in the diet of naturally occurring black-backed jackal (Grafton, 1965; du P Bothma, 1971; Kaunda and Skinner, 2003).

In summer, anthropogenic items, mammals and other unidentifiable components were recorded at minimal levels. For the reasons mentioned above, the amount of anthropogenic matter in the diet of the jackal may also have been underrepresented in summer, resulting in the low occurrence in scats. The lower than expected occurrence of mammal components in summer may be due to black-backed jackals feeding patterns which show an inclination for prey that is more energetically and nutritionally easier to catch (Klare et al., 2010), such as the ground-dwelling hatchlings.

Black-backed jackal are urban adapters

As far as I am aware, my study is the first to investigate the ecology of black-backed jackals in an urban environment. Carnivores display various adaptations to life in urban environments, including changes in activity patterns and diet (Bateman and Fleming, 2012). The extent of these adaptations can impact the success of a species (Jung and Kalko, 2010; Sih et al., 2011). Behavioural adjustments, such as behavioural flexibility, can play a critical functional role in the success of animals exploiting urban environments (Lowry et al., 2012; Sol et al., 2013; Dammhahn et al., 2020).

From my results, it would appear that the black-backed jackals at the Estate are showing a change in some components of their biology compared with their naturally occurring counterparts. Their daily and seasonal activity profile was shifted, possibly in response to human activity and to exploit alternative food resources offered in urban environments. For urban mammals to successfully cope with the risks and novelty of urban environments such as conflict with humans and traversing roads, they alter their activity and foraging patterns to times of lowest human activity (Lowry et al., 2012). Some of the behaviours of the black-backed jackal at the Estate showed similar seasonal variation but adjustments temporally were minimal. Although the black-backed jackals at the Estate maintained a wide diet breadth, as recorded in naturally occurring black-backed jackals, the nature of their diet incorporated the different food resources available in their urban environment. This generalist nature, a feature common in urban wildlife (Chace and Walsh, 2006; Sih, 2013), facilitates their adaptation to novel urban environments.

The black-backed jackals at the Estate did not seem to fully exploit all the advantages urban environments may offer but show changes that suggest that they may be more characteristic of urban adapters. Urban adapters are defined as species that are able to adapt to urban areas while still making use of natural resources (Bateman and Fleming, 2012). However, it is possible that should urban adapters become isolated from natural areas, they could become ‘obligate’ exploiters – being forced to utilize any available resources in order to survive. The black-backed jackals at the Estate used the natural spaces offered by the golf course at the Estate while modifying their diet and behaviour to the presence of humans, although they also showed a high level of habituation to people (e.g. are visible on the golf course during the day). If these small changes in the black-backed jackals' ecology in the urban environment continue, they may result in broader changes, allowing them to attain greater population densities and maintain smaller home ranges, as seen in stone martens in

some towns in Luxembourg (Herr et al., 2009). These stone martens show densities of up to 6 adults/km^2, compared with rural stone martens whose densities are recorded as 0.7-2.0 adults/km^2 while maintaining home ranges of 37 ha and 113 ha for females and males respectively compared with 75 ha and 880 ha for females and males respectively in a forest environment (Herr et al., 2009). Naturally-occurring black-backed jackals occur at densities of 0.37 individuals/km^2 in Pilanesberg National Park, South Africa (Yarnell et al., 2013), to 9.8 individuals/km^2 in Cape Cross Seal Reserve, Namibia (Jenner et al., 2011). Environmental conditions, such as food resources, appear to impact the size and use of home ranges, as well as densities of black-backed jackals (Kaunda, 2000; Jenner et al., 2011; Nattrass et al., 2017). In the Estate, the population fluctuates on an annual basis between 20-24 jackals, giving a population density of 12.05-14.46 individuals/km^2. This shows a greater population density compared with their naturally occurring counterparts.

CONCLUSION

In my study of urban black-backed jackals, I assessed their seasonal and diel activity patterns and diet, considering their diet breadth and the possible incorporation of anthropogenic foods at the Jackal Creek Golf Estate. I found that the jackals appear to be displaying small changes in all the variables I measured, and so showing a degree of plasticity as a result of the novel urban environment that they now inhabit (Gese and Bekoff, 2004). What we are seeing is an animal that has the characteristics of an urban adapter, and that if given the opportunity, has the potential to become an urban exploiter, i.e. an animal that purposefully occupies and utilises urban environments and any associated anthropogenic foods (Bateman and Fleming, 2012). The benefits of an urban environment together with the generalist nature of the diet and habits of black-backed jackals may be key to them achieving greater population densities and allowing them to persist in urban environments (Theimer et al., 2015). The concern of course is that greater black-backed jackal densities in urban areas might result in potential human-wildlife conflict. Black-backed jackals have a long history of conflict with farmers as a result of their penchant for livestock (Humphries et al., 2015; Minnie et al., 2016), as well their bad reputation as vectors of diseases such as rabies (McKenzie, 1993; Minnie et al., 2016). Conflict with wildlife increases with increasing proximity to human habitation, resulting in a need for managing the conflict (Ditchkoff et al., 2006). Conflict with coyotes living in the metropolitan area of Denver, USA has been

recorded on varying levels, including incidents (cases of coyotes exhibiting agonistic behaviours towards humans), pet-attacks and human-attacks (most commonly as a result of interference during pet-attacks) (Poessel et al., 2013; Breck et al., 2019). Brown rats (*Rattus norvegicus*), an abundant animal in urban areas throughout the world, are in regular conflict with humans due to the damage they cause to property and their role in the spread of zoonotic diseases (Murray et al., 2018). Human-wildlife conflicts are often associated with the feeding of wildlife by humans, leading to attacks on humans by animals, as occurs in dingoes in urban areas (Cox and Gaston, 2018).

An additional objective of my study was to determine the current distribution of black-backed jackals in the Greater Johannesburg area, which unfortunately yielded insufficient data to reach meaningful conclusions on the extent of their urban occurrence in urban Greater Johannesburg. Black-backed jackals in peri-urban and urban areas may be an emergent issue requiring additional investigation. Without additional study sites, my study at Jackal Creek Golf Estate provides foundational information (i.e. a case study) that could be useful for future studies of black-backed jackals elsewhere, should they exploit urban areas. More focussed studies on the species distribution may be required in the future. Further studies could incorporate the evaluation of environmental impact studies conducted by developers prior to construction in outlying areas of Johannesburg to assess the presence of black-backed jackals in these areas. This may highlight whether jackals are moving into these areas or becoming trapped as a result of the development, an important question that needs to be answered with regard to urban wildlife (Gehrt et al., 2009).

Additional research into the factors that affect the activity patterns of the black-backed jackal at the Estate is also required. Future studies should investigate the home range use and size of established breeding pairs within the Estate, such as through radio tracking individuals. Such studies were not possible in my study because I could not obtain permission to capture and mark the jackals. More detailed studies into the diet of the jackals at the Estate could also be conducted, such as through DNA metabarcoding which will also give an indication of the local biodiversity of the Estate (de Sousa et al., 2019). Other studies on this population of black-backed jackals could include the cataloguing of birth rate per breeding pair to determine reproductive success and dispersal patterns and a more accurate demography of the black-backed jackals at the Estate. Finally, the relatively stable population size of 20-24 jackals at the Estate suggests that adult offspring disperse into neighbouring areas, but their circumstances post-dispersal is unknown and requires follow up studies to

establish whether they disperse into other urban areas or into natural areas in close proximity to the Estate.

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SUPPLEMENTARY MATERIAL

Supplementary 1. Contribution of each behaviour to Chi-squared analysis for time period 'Night' (00h00 to 06h00) and 'Evening/Night' (18h00 to 24h00) respectively.

	Behaviour						
	Aggression	**Forage**	**Play**	**Rest**	**Affiliative**	**Travel**	**Other**
Winter	0.408	0.387	0.816	1.355	0.676	-1.817	0.243
Summer	-0.858	-0.814	-1.717	-2.851	-1.423	3.824	-0.511

	Behaviour						
	Aggression	**Forage**	**Play**	**Rest**	**Affiliative**	**Travel**	**Other**
Winter	0.524	0.428	0.801	1.057	0.646	-1.221	0.503
Summer	-1.074	-0.877	-1.641	-2.166	-1.323	2.502	-1.031

Supplementary 2. Contribution of each behaviour to Chi-squared analysis for time period 'Morning' (06h00 to 12h00) and 'Afternoon' (12h00 to 18h00) respectively.

	Behaviour						
	Aggression	**Forage**	**Play**	**Rest**	**Affiliative**	**Travel**	**Other**
Winter	0.066	0.104	0.132	0.154	0.066	-0.176	0.0466
Summer	-0.302	-0.477	-0.603	-0.707	-0.302	0.805	-0.213

	Behaviour					
	Forage	**Play**	**Rest**	**Affiliative**	**Travel**	**Other**
Winter	0.143	0.143	0.591	0.143	-0.382	0.203
Summer	-0.365	-0.365	-1.506	-0.365	0.974	-0.516

Supplementary 3. Pairwise Chi-squared comparisons between categories of foods eaten by jackals at the Jackal Creek Golf Estate in winter and summer 2019/2020 as per numerical frequency scat analysis.

Summer	**Winter**	**χ^2 value**	**Degrees of freedom**	**p-value**
Anthropogenic	Anthropogenic	0.00	1	0.947
Mammals	Mammals	0.10	1	0.756
Birds	Birds	0.21	1	0.645
Arthropods	Arthropods	2.00	1	0.158
Unidentifiable vertebrates	Unidentifiable vertebrates	0.16	1	0.687
Monocots	Monocots	0.01	1	0.912
Dicots	Dicots	0.30	1	0.581
Fruits/Seeds	Fruits/Seeds	0.02	1	0.890
Other	Other	1.80	1	0.180

Supplementary 4. Pairwise Chi-squared comparisons between categories of foods eaten by jackals at the Jackal Creek Golf Estate in winter and summer 2019/2020 as per percentage mass contribution scat analysis.

Summer	Winter	χ^2 value	Degrees of freedom	p-value
Anthropogenic	Anthropogenic	0.58	1	0.445
Mammals	Mammals	0.17	1	0.679
Birds	Birds	0.05	1	0.818
Arthropods	Arthropods	0.32	1	0.570
Unidentifiable vertebrates	Unidentifiable vertebrates	1.48	1	0.223
Monocots	Monocots	0.51	1	0.477
Dicots	Dicots	0.03	1	0.859
Fruits/Seeds	Fruits/Seeds	0.21	1	0.647
Other	Other	0.58	1	0.446

Supplementary 5. Pairwise Chi-squared comparisons between categories of foods eaten by jackals at the Jackal Creek Golf Estate in winter and summer 2019/2020 as per all methods of scat analysis.

Pairwise test	χ^2 value	Degrees of freedom	p-value
Frequency of occurrence	22.70	8	0.004
Numerical frequency	4.61	8	0.799
Percentage mass contribution	3.94	8	0.863

Supplementary 6. Pairwise Chi-squared comparisons between categories of foods eaten by jackals at the Jackal Creek Golf Estate in winter and summer 2019/2020 as per the frequency of occurrence scat analysis.

Summer	Winter	χ^2 value	Degrees of freedom	p-value
Anthropogenic	Anthropogenic	0.05	1	0.828
Mammals	Mammals	1.07	1	0.300
Birds	Birds	0.44	1	0.508
Arthropods	Arthropods	7.76	1	0.005
Unidentifiable vertebrates	Unidentifiable vertebrates	0.20	1	0.652
Monocots	Monocots	0.57	1	0.449
Dicots	Dicots	2.74	1	0.098
Fruits/Seeds	Fruits/Seeds	0.00	1	0.984
Other	Other	11.26	1	0.001

APPENDICES

Appendix 1

An example of the Google form questionnaire that was circulated through Facebook to members of the public of the Greater Johannesburg area to report any black-backed jackal sightings in order to determine the current species distribution.

Jackal Watch Joburg

My name is Carina Wilkins, a Johannesburg resident and citizen scientist. With this survey I would like to establish where black-backed jackal (Canis mesomelas) occur within the greater Johannesburg area, and whether they are successfully living in and around urban centres.

Consent to participate:

- I confirm that I have read and understand the Participant Information Sheet
- I have had the opportunity to ask questions and have had them answered
- I understand that all personal information will remain confidential
- I agree that data gathered in this study may be stored anonymously and securely, and may be used for future research
- I understand that my participation is voluntary and I am free to withdraw my participation BEFORE submission
- I understand that once submitted I have given final consent to take part in the study

Consent *

Do you consent to participate in this survey?

☐ Yes

☐ No

Question 1

Have you personally seen black-backed jackal in the greater Johannesburg area?

☐ Yes

☐ No

Question 2

If you answered yes to question 1, can you recall how many you saw together in one sighting?

- [ ] 1 individual
- [ ] 2 individuals
- [ ] 3-5 individuals
- [ ] >5 individuals

Question 3

If you answered yes to question 1, can you recall if there were puppies?

- ◯ Yes
- ◯ No

Question 4

If you answered yes to question 1 and/or 3, can you provide the GPS co-ordinates or a physical address for the location at which you saw them.

Long answer text