Scientific Assessment on Livestock Predation in South Africa

CHAPTER 8

THE ROLE OF MESO-PREDATORS IN ECOSYSTEMS: POTENTIAL EFFECTS OF MANAGING THEIR POPULATIONS ON ECOSYSTEM PROCESSES AND BIODIVERSITY

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Introduction

Predators have considerable impacts on ecosystems and biodiversity, with many recent studies highlighting their strong top-down effects that influence ecosystem structure and function. The majority of this understanding comes from a handful of studies on large charismatic apex predators (Roemer *et al.* 2009; Ripple *et al.* 2014). Apex predators can have a large impact on ecosystems and their removal has a disproportionately disruptive influence on ecosystem structure and function (Ripple *et al.* 2014). However, most predators are neither large nor charismatic and consequently have received relatively little research attention compared with the small group of apex predators upon which much research time and funding are focused (Roemer *et al.* 2009). These small- to medium-sized predators, collectively called mesopredators, are often capable of living close to humans and can attain population densities considerably greater than that of apex predators (DeLong and Vasseur 2012). Through their combined influence, small to medium sized predators have the capacity to influence ecosystems (Roemer *et al.* 2009). Despite this, we know very little about their ecological roles and how fluctuations in their abundance influence biodiversity.

In natural ecosystems, where present, large predators can regulate the abundance and, therefore, the impact that mesopredators may have on ecosystems and biodiversity (Crooks and Soulé 1999; Morris and Letnic 2017). In the absence of apex predators, mesopredators alter their foraging behaviour and may increase in abundance through a process known as mesopredator release (Soulé *et al.* 1988), and are often synthetically elevated to the position of top predators in ecosystems.

In human dominated landscapes, large tracts of land are being used for agriculture and human habitation, with those areas cleared for agriculture placed under varying intensities of stock and crop production (Osinubi *et al.* 2016). Furthermore, landscape conversions are often associated with a simplification of the faunal and floral assemblages, often in association with the loss of apex predators. Therefore, in the Anthropocene, mesopredators exist under circumstances of multiple land-use types, fulfilling a myriad of ecological roles (Prugh *et al.* 2009).

In South Africa, this variable and context-dependent trophic status of mesopredators prevails, as some ecosystems retain large predators, some ecosystems are largely intact despite the absence of large predators, and some ecosystems are completely altered and simplified for agricultural purposes (Figure 1). In agricultural landscapes, mesopredator persecution might replace the regulatory impacts of extirpated apex predators. However, it is not fully understood how human persecution differs from top-down regulation by apex predators given the spectrum of control options used to combat problem causing animals (See Chapter 4). Considering the diverse array of land uses and the long history of problem animal persecution in South Africa (See Chapter 2), it would be reasonable to expect that ample research has been conducted on the ecological role of mesopredators across this ecosystem continuum. This is, however, far from the reality, and our current understanding of the role of these predators in various ecosystems in South Africa is poor (du Plessis *et al.* 2015). We are only starting to understand mesopredator biology (See Chapter 7), let alone the complex interactions that mesopredators have with sympatric biota. This fundamental lack of information has hindered management; this is exemplified by the myriad of largely ineffective control measures deployed to reduce the impact by mesopredators on livestock in South Africa (Chapter 4).

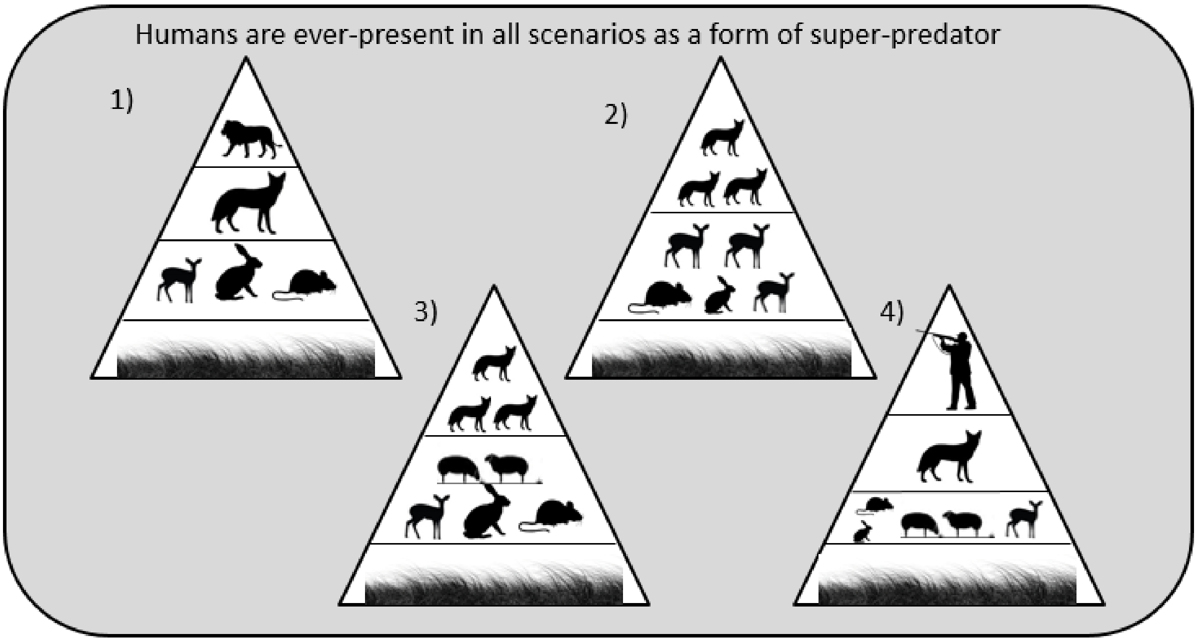

Figure 8.1: Graphical representation of various ecosystems in South Africa; 1) an intact ecosystem where apex predators are present and mesopredators consume a range of wild small ungulates, rodents and lagomorphs which in turn feed on vegetation, 2) an ecosystem where apex predators have been extirpated and mesopredators are released from top-down control and consume large prey along with rodents and lagomorphs which in turn feed on vegetation, 3) a modified ecosystem where apex predators have been extirpated and mesopredators are released from top-down control and consume ungulates, rodents, lagomorphs and livestock which in turn feed on vegetation, 4) a highly modified ecosystem where apex predators have been extirpated, mesopredators are persecuted by humans while feeding on a range of ungulates, rodents, lagomorphs and livestock which in turn feed on vegetation. For all scenario’s, silhouette size has no meaning and only the number of jackal silhouettes reflect abundance (greater jackal abundance expected where top-down control is lacking).

In this chapter we investigate the ecological role of mesopredators in relation to their position in the food web (apex or mesopredator) and the complexity of the ecosystem (agricultural landscapes or natural ecosystems). In addition, we consider the impact that humans may play in filling the role of apex predators in ecosystems where apex predators have been extirpated. We start by identifying the ecological roles of mesopredators and then try to elucidate the functional roles of black-backed jackal *Canis mesomelas* and caracal *Caracal caracal* in South Africa. However, although basic information exists for these species' diets (See Chapter 7), available scientific information relating to their functional roles in ecosystems is limited. We will therefore draw on available information from the functional roles of related taxa (or ecological surrogates) to infer possible additional ecological roles of mesopredators across southern African ecosystems.

We therefore aim to assess the following;

- What are the functional roles of mesopredators (global scale)?
- What are the functional roles of black-backed jackals and caracal in South African ecosystems?
- What can we learn from international canid and felid research that may be relevant to understanding black-backed jackal and caracal functional roles in South Africa?
- What are the predicted / possible biodiversity implications (direct and indirect) of attempting to remove black-backed jackal and caracal from farmlands in South Africa?

By highlighting these issues, we will further explore what information is needed to understand the functional role that two ubiquitous mesopredators play in South African ecosystems, namely black-backed jackal and caracal.

<u>Role of mesopredators in ecosystems</u>

Mesopredators generally weigh less than 20 kg (see Carbone *et al.* 2007; Prugh *et al.* 2009; Ripple *et al.* 2014; Wallach *et al.* 2015 for specific weight thresholds) and their populations can be regulated through top-down control by larger predators (i.e. apex predators for many mesopredators, Prugh *et al.* 2009; Ritchie and Johnson 2009) as well as through bottom up processes like food availability (López-Bao *et al.* 2010). In habitats devoid of apex predators, human persecution of mesopredators could replace this regulatory role of apex predators. However, due to mesopredators' often wide and adaptable diet, ability to live close to humans and their capacity for high population growth rates, humans often struggle to regulate their numbers (Dorresteijn *et al.* 2015). Where top-down control does happen, this often limits the ecological impact that mesopredators have on ecosystems and sympatric biodiversity (Berger and Conner 2008; Ritchie and Johnson 2009). However, where top-down regulation of mesopredators is absent, mesopredator release may occur, with mesopredators increasing in abundance and ultimately changing their impacts on the ecosystem (Courchamp *et al.* 1999; Crooks and Soulé 1999; Ritchie and Johnson 2009). Under these conditions, mesopredators become the top predators in ecosystems; however, due to allometric constraints related to prey body size their impacts may not extend to very large prey species. The resulting elevation of mesopredator to top predator status coincides with top down regulation on a range of species on parallel and lower trophic levels (Myers *et al.* 2007). The discussion below, on the role of mesopredators in ecosystems, includes their ecological roles in; a) intact systems where large apex predators are present and b) systems where apex predators have been lost. We conclude our discussion of mesopredator ecological roles by highlighting the roles that ecological complexity (i.e. predator and prey diversity and species richness) and productivity play in modulating the effects of mesopredator function in ecosystems.

Mesopredators' ecological roles under top-down regulation by apex predators: Mesopredators are important drivers of ecosystem function, structure and dynamics. Due to metabolic scaling (Carbone *et al.* 2007), mesopredators regulate prey populations that are not regulated by large predators and the latter may also regulate prey populations that mesopredators are unable to regulate. Small predators (< 20 kg) can subsist on a diet of invertebrates, plants and small vertebrate prey, whereas larger predators need to consume large vertebrate prey to meet metabolic requirements (Carbone *et al.* 1999). Thus, mesopredators are important predators of small vertebrates (i.e. lagomorphs, birds and rodents), including pest species (Newsome 1990), and can indirectly shape plant communities through predation on seed predators (Asquith *et al.* 1997; DeMattia *et al.* 2004) or by directly dispersing seeds themselves (Silverstein 2005; Jordano *et al.* 2007).

Many mesopredators are facultative scavengers that provide valuable ecosystem services in the form of waste removal (Ćirović *et al.* 2016). Mesopredators can be important reservoirs of diseases which may negatively impact humans (e.g. bat-eared foxed *Otocyon megalotis* can transmit rabies) (Thomson and Meredith 1993), domestic and wild ungulates (e.g. Bovine tuberculosis spread by badgers *Meles meles*) (Woodroffe *et al.* 2006) and sympatric predators (Hennessy *et al.* 2015). The transmission of pathogens to the relatively smaller populations of apex predators can be ecologically devastating, as large predators may be more vulnerable to stochastic disease outbreaks (Kissui and Packer 2004). The introduction of canine parvovirus from dogs *Canis familiaris* into the gray wolf *Canis lupus* population on Isle Royale led to a decline in wolf numbers, resulting in a switch from predator regulation to food regulation of the moose *Alces alces* population (Wilmers *et al.* 2006). However, mesopredators could also indirectly protect human health by reducing population size of rodent reservoirs of human disease (Ostfeld and Holt 2004).

Mesopredators can be important links between ecological communities by directly thwarting or facilitating nutrient subsidies (Roemer *et al.* 2009). For example, river otters *Lontra canadensis* link aquatic and terrestrial communities through their latrines (depositing aquatically-derived nutrients on terrestrial landscapes) (Ben-David *et al.* 2005; Crait and Ben-David 2007).

Mesopredator ecological roles without apex predator regulation: With large terrestrial mammalian carnivores having declined by 95-99% globally (Berger *et al.* 2001; Ripple *et al.* 2014) we are now experiencing important changes in trophic dynamics and community organization (Ritchie and Johnson 2009). Following apex predator removal, mesopredator release often occurs. Under these circumstances, along with maintaining their functional role as described above, mesopredators can also assume the ecological role of *de facto* apex predators through direct predation effects and indirect fear-driven effects at multiple trophic levels when they exist (Palomares and Caro 1999; Ripple and Beschta 2004). Thus following mesopredator release, there is often an increase in predation pressure and a reduction in biodiversity (Wallach *et al.* 2015). One of the most studied consequences of mesopredator release is the impact that dominant mesopredators have on subordinate sympatric mesopredators. During mesopredator release, dominant mesopredators increase in abundance if they are not regulated by bottom-up processes (see ecosystem complexity below), often negatively impacting smaller predators. In contrast, when apex predators are re-established, the abundance of the dominant mesopredator often declines, cascading into the increase of smaller predators with ecosystem shifts taking place. For example, on the California Channel Islands, the island fox *Urocyon littoralis* was the top predator and inhibited its only competitor, the island spotted skunk *Spilogale gracilis amphiala*. However, following the arrival of golden eagles *Aquila chrysaetos*, a superior predator, island fox abundance declined which precipitated an increase in spotted skunk abundance (Roemer *et al.* 2002).

Much ecosystem destabilisation is the direct result of anthropogenic disturbances. Considering anthropic impacts on ecosystems, mesopredators' ascension to top predator status is likely to become more common and it is crucial to recognize this when drafting management and conservation plans. It is also important that research be designed, and implemented, to take advantage of the loss or reintroduction of apex predators to increase our understanding of the interacting roles of predators in ecosystems. The difference in the impact of mesopredators when filling the functional role of meso- vs top-level predators is at times quite stark. As mesopredators, feral cats *Felis catus* are predators of small prey species such as rodents, lizards and birds in many continental ecosystems (Crooks and Soulé 1999; Doherty *et al.* 2015). However, where cats have been introduced onto islands, they are often the top predator and can cause severe declines in prey populations (Medina *et al.* 2011). The ecological impact of cats is most pronounced when they are an invasive species and not regulated by apex predators. Mesopredator release also has the potential to lead to the extinction of certain prey species (Soulé *et al.* 1988; Palomares *et al.* 1995; Burbidge and Manly 2002), particularly those with low population growth rates or those that are susceptible to mesopredator predation (Courchamp *et al.* 1999). For example, on the Virginia barrier islands (USA), the presence of racoon *Procyon lotor* and red fox *Vulpes vulpes* are major obstacles for the recovery and conservation of beach-nesting and colonial waterbirds (Porter *et al.* 2015).

In many agricultural systems, historic top-down regulation of mesopredators due to apex predators can partially be replaced by persecution by humans. Furthermore, mesopredator prey assemblages are supplemented with domestic animals. Top-down effects by humans seldom replicate the full suite of regulative influences that apex predators exert on mesopredators (Peckarsky *et al.* 2008) and prey resource supplementation through livestock husbandry may reduce bottom-up constraints. However, the addition of livestock to the system may also negatively affect wild ungulates (Ripple *et al.* 2015) and rodents (Eccard *et al.* 2000) through competition for resources and therefore lower the natural prey availability to mesopredators, possibly increasing bottom-up constraints. Agricultural landscapes are often simple linear food chains (see ecological complexity below); with either mesopredator hyper-abundance (release) or extermination likely to have pervasive ecological effects (Roemer *et al.* 2009). Mesopredator release may result in pest problems for both commercial and small-scale small-livestock enterprises. Across South Africa, the extirpation of large predators on farmlands, along with the expansion of agricultural practices, is thought to have led to increases in black-backed jackal and caracal populations, potentially creating bigger challenges in terms of livestock depredation (Humphries *et al.* 2015; Kerley *et al.* 2017).

In urban landscapes where development is intensive and humans do not regulate mesopredators, mesopredators exploit the niche space vacated by apex predators (Prugh *et al.* 2009). For example, in coastal southern California, most of the native sage-scrub habitat has been destroyed leading to the local decline of the most common large predator, the coyote *Canis latrans* (Crooks and Soulé 1999). Lower coyote abundances and increased anthropogenic food availability have resulted in release of various native mesopredators including the striped skunk *Mephitis mephitis*, racoon, grey fox *Urocyon cinereoargenteus,* domestic cat and Virginia opossum *Didelphis virginiana* (Crooks and Soulé 1999). The release of these predators from top-down control has led to increased mortality of prey species of these smaller predators.

Ecological productivity and complexity and carnivore diversity modulating ecosystem impacts of mesopredators: In many ecosystems, untangling the relative influence that bottom-up versus top-down effects have on mesopredator abundance is difficult. Bottom-up effects can include both ecosystem productivity (i.e. resource availability) and complexity (number of links and interactions in food webs). For example, during agricultural expansion in Sweden, apex predators (wolf and Eurasian lynx *Lynx lynx*) numbers declined. Consequently, in productive habitats, red fox population growth rates increased considerably following the relaxation of regulation by apex predators. In contrast, in low productivity habitats, red fox population growth rates showed little change following apex predator extirpation (Elmhagen and Rushton 2007). Low productivity environments are often characterised by considerable variation in climate and resource abundance, with abiotic factors often playing a larger role in structuring ecosystems than biotic interactions (Roemer *et al.* 2009). In particular, rodent abundance (an important resource for many mesopredators) in arid and semi-arid regions is more strongly influenced by rainfall variation than predation (Jaksic *et al.* 1997), limiting the cascading impact that mesopredators could have. Therefore, ecosystem productivity may play a key role in governing the magnitude of the response from mesopredators following the removal of the regulation from apex predators.

Contrasting responses and impacts of mesopredators on ecosystems may reflect the complexity of the habitat that the mesopredator occupies. Mesopredators have larger impacts in simple linear ecosystems than on complex ecosystems (Roemer *et al.* 2009). For example, in the diverse Atlantic forests, the loss of jaguars *Panthera onca* and pumas *Puma concolor* has resulted in the ocelot *Leopardus pardalis* being elevated to the highest-ranking predator in these forest patches. However, in these forest ecosystems, ocelots do not appear to have significant detrimental impacts on sympatric mesopredators (Massara *et al.* 2016). Similarly, mesopredator release may be less prevalent in ecosystems with many competing mesopredators with overlapping niches such as in South Africa. In contrast, the introduction of cats onto islands that are characterised by simple linear food webs results in strong top-down control of the native mesopredators and prey species with observable knock-on effects for biodiversity (Medina *et al.* 2011). Thus, the impacts of predator rearrangement in complex systems may have greater time lags for observable ecological changes than relatively simple linear ecosystems with fewer mesopredator species. Ecosystem productivity and complexity may be important in governing mesopredator responses to reduced regulation of mesopredators in agricultural ecosystems (discussed later). It is likely that ecosystem productivity and complexity (including predator diversity and species richness), will determine the relative strength and direction of interactions among predators through food availability, habitat structure and complexity of food webs. The roles of mesopredators in ecosystems is therefore context-dependent and a result of complex interactions between top-down and bottom-up factors (Monterroso *et al.* 2016).

Role of black-backed jackals in ecosystems

Understanding the role of black-backed jackals (10.3 kg: mean weight - taken from Wallach *et al.* 2015) in ecosystems in southern Africa is challenging due to their elusive nature (James *et al.* 2015). Despite the long-standing problem of black-backed jackal predation on livestock, our understanding of their ecology has seldom extended beyond that of cursory single species investigations of diet, activity patterns, and only recently, genetics and reproduction (See Chapter 5). Single species studies hinder our ability to understand the role that black-backed jackals play in ecosystems and their impact on sympatric biodiversity. Faced with the daunting task of unpacking the ecological role of black-backed jackals, starting with the diet (the most well studied component of black-backed jackal biology – see chapter 5) seems logical.

Black-backed jackals are omnivorous, with diets varying widely in relation to food availability. Across most of their range, black-backed jackals prefer smaller ungulates that hide their young while avoiding both larger ungulates that hide their young and ungulates whose young follow the parents from an early age (Klare *et al.* 2010; Hayward *et al.* 2017). Hayward and colleagues further suggest that black-backed jackal diets are influenced by both top-down (apex predator presence or absence) and bottom-up (prey size and life history pattern) processes. At high black-backed jackal densities, which can occur under conditions of high resource availability (Oosthuizen *et al.* 1997; Jenner *et al.* 2011; Yarnell *et al.* 2015) and reduced competition, as is also the case for golden jackal *Canis aureus* (Singh *et al.* 2016), black-backed jackals exhibiting the above preference strategy may limit populations of small ungulates that employ a hider strategy (Morwe 2013). Black-backed jackals have been seen to regulate populations of springbok *Antidorcus marsupialis* in the Northern Cape, South Africa (Klare *et al.* 2010; Morwe 2013) and blesbok *Damaliscus pygargus* in the Highveld of South Africa (du Plessis 1972). In contrast, in the presence of apex predators, and consequential carrion provisioning, peaks in the availability of juvenile ungulates appear to be less important for foraging black-backed jackals (Van de Ven *et al.* 2013; Gerber 2014) potentially limiting jackal impacts. Contrasting landscapes and / or time periods with and without apex predators provide conflicting perspectives on whether black-backed jackals adjust their foraging behaviour in the presence or absence of large carrion-providing predators (Brassine and Parker 2012; Yarnell *et al.* 2013; Fourie *et al.* 2015; Hayward *et al.* 2017). Thus, it is unknown whether black-backed jackals will regulate populations of small to medium sized ungulates when additional food sources like carrion or livestock are provided.

On farmlands, black-backed jackals are effective predators of livestock (Kamler *et al.* 2012a; Humphries *et al.* 2016), taking advantage of the reduced anti-predator behavioural responses in domesticated species (Mabille *et al.* 2016). Sheep *Ovies aries* and goats *Capra* *hircus* can comprise up to 48% of black-backed jackal diets and their consumption tends to peak during the lambing season (Kamler *et al.* 2012a; Pohl 2015) and may be dependent on the farming practice employed (Humphries *et al.* 2015). Thus, the pattern of consumption of livestock by black-backed jackal seems to mimic the patterns exhibited when black-backed jackals consume ungulates in the absence of apex predators. However, despite their consumption of livestock, it remains unclear whether jackals select wild prey more than domestic prey (Northern Cape - Kamler *et al.* 2012a; Southern Free State - Pohl 2015) or domestic prey more than wild prey (Central Karoo; Drouilly et al. In Review). The relative consumption of wild versus domestic prey may however also be dependent on the composition of wild prey available to black-backed jackal.

Although black-backed jackals hunt and consume small rodents (Hayward et al. 2017), there is no evidence that such consumption provides viable long term pest control services where rodents are crop pests (Swanepoel *et al.* 2017). However, whereas most rodents have eruptive life-history characteristics, some, like mole rats (e.g. African mole-rat *Cryptomys hottentotus*), may have lower reproductive potential (Skinner and Chimimba 2005) and therefore be more susceptible to top-down regulation. The difference in regulatory ability of black-backed jackals to rodents with slow versus fast life-history characteristics has however received no attention. Predators of rodents can be distinguished as either specialists or generalists. Generalist predators have access to and use a variety of prey. This habit characterises black-backed jackals and other larger mesopredators discussed in this chapter. Generalist predators tend to stabilise rodent prey populations, although much of the available literature on these dynamics comes from northern temperate regions (Andersson and Erlinge 1977). In contrast, specialist rodent predators like African wild cat *Felis lybica* (Palmer and Fairall 1988), which are often regulated by black-backed jackals (Kamler *et al.* 2012b) are likely to destabilize rodent populations (Andersson and Erlinge 1977). Since much of the available information on predator-rodent interactions comes from northern temperate regions, it remains to be seen whether black-backed jackals stabilise or destabilise impacts on rodent populations or whether bottom-up processes are more important than predation in South Africa.

In many ecosystems in South Africa, black-backed jackals are the dominant predator, especially in landscapes where apex predators have been extirpated (Klare *et al.* 2010). When cast in this dominant role, black-backed jackals seem to suppress populations of smaller and less competitive mesopredators including bat-eared fox *Otocyon megalotis*, Cape fox *Vulpes chama*, many mongoose species (Kamler *et al.* 2012b; Bagniewska and Kamler 2014), black-footed cat *Felis negripes* (Kamler *et al.* 2015) and large spotted genet *Genetta tigrina* (Ramesh and Downs 2014). On farms in the Kalahari where persecution of black-backed jackal is relatively high, the relative abundances of sympatric mesopredators including bat-eared fox, cape fox and small spotted-genet *Genetta genetta* are higher than in areas where there are lower levels of human management of black-backed jackals (Blaum *et al.* 2009). Along with direct mortality, black-backed jackals may influence bat-eared foxes in non-lethal ways, recent evidence suggests that bat-eared foxes are more wary in dark conditions with potential foraging implications (Welch *et al.* 2017). The direct link between black-backed jackal activity and the observed response from bat-eared foxes is not yet clear, but this research may begin to illuminate some of the non-lethal impacts that black-backed jackals might have on smaller carnivores. These observations were made in the absence of large predators, and whether black-backed jackals have the same impacts (lethal and non-lethal) when they occur in sympatry with large apex predators is unknown.

Black-backed jackals are facultative scavengers and undoubtedly play a role in carrion removal (otherwise known as waste removal as mentioned earlier) on the landscape. In African landscapes, black-backed jackals compete with potentially dominant scavengers (i.e. spotted hyaena *Crocuta crocuta* (Hunter *et al.* 2007) and brown hyaena *Hyaena brunnea* (Ramnanan *et al.* 2016)) and where they occur sympatrically with larger scavengers, black-backed jackals may be more reliant on other food sources (Ramnanan *et al.* 2016). Therefore, although they play important roles in waste removal, they may not be as important as golden jackals have been observed to be in Europe (see below). Both black-backed jackals and side-striped jackals *Canis adustus* are possible reservoirs for rabies (Butler *et al.* 2004), with populations at high densities capable of sustaining disease outbreaks (Cumming 1982). These disease outbreaks can have societal (spread of rabies to domestic and communal land dogs - Butler *et al.* 2004) and conservation (spread of rabies to apex predator populations - Hofmeyr *et al.* 2004) implications.

The limited scientific understanding of the larger ecological effects of black-backed jackals has recently come under the spotlight, with a review published in 2015 suggesting that published knowledge on black-backed jackals is limited in scope, geographic location and in most cases dated (appearing before 2005; du Plessis *et al.* 2015). Moreover, most of the studies that have been conducted were in protected areas, limiting the application of the findings to protected areas. Most of the questions raised by this review, however, focused on the biology of black-backed jackals and caracals and these deficiencies are addressed in chapter 7. As for many other mesopredators, the role that black-backed jackals play in the ecosystem is context-dependent (Fourie *et al.* 2015), based on the interaction of top-down and bottom-up forces that drive the relative availability of resources. Armed with a catholic diet and a plastic behavioural repertoire, black-backed jackals have the ability to modify their diet, limiting our ability to predict the functional response of black-backed jackals to landscape-level changes or manipulations.

Additional ecosystem functions of black-backed jackal surrogates

Across the globe, a number of canids occupy similar niches to black-backed jackals. In particular, we will focus on four key species, the golden jackal (11 kg), coyote (13.3 kg), dingo (16.5 kg) and red fox (4.1 kg; weights represent average weights taken from Wallach *et al.* 2015). It is likely that these species have similar ecological roles to black-backed jackals and we can infer potential black-backed jackal ecosystem roles from these species.

Direct impacts on prey species: Canid mesopredators, in particular golden jackals and red foxes, play an important role in the regulation of small prey species such as lagomorphs and rodents (Lanszki *et al.* 2006; Dell'Arte *et al.* 2007). In Europe, golden jackals are estimated to consume 158 million crop pests a year (Ćirović *et al.* 2016); undoubtedly limiting the damage these species have in agricultural ecosystems. In Australia, red fox expansion has coincided with declines in populations of small- and medium-sized mammals (Saunders *et al.* 2010; Woinarski *et al.* 2015) indicating that not only do these mesopredators regulate small prey, but, under certain conditions (i.e. simplified ecosystems with low productivity and few competing carnivores), reduce prey populations. However, prey population declines in Australia may be the result of different evolutionary paths for those predators and prey. Australian prey did not evolve alongside red foxes (or domestic cats); therefore, where predator and prey have evolved together, as is the case with black-backed jackal and their prey, the impacts of predation may not be as severe. Many of these small- and medium-sized prey species in Australia are important seed predators and increased predation by red foxes have had observable impacts on the composition of the vegetation (Gordon *et al.* 2017 - see below). In North America, coyotes are similarly important predators of lagomorphs. In many farming areas, the persecution of coyotes has resulted in an increase in the competition between lagomorphs and cattle; with the impacts of lagomorph competition exceeding the impact that predation by coyotes would have on cattle populations (Ranglack *et al.* 2015). Although black-backed jackals consume many similar small prey species, the extent of their population regulatory ability remains largely unknown.

Birds may form an important part of red fox, golden jackal and coyote diets across much of their range particularly during the nesting season when ground-nesting birds may be susceptible to nest and chick predation. Coyote predation on birds at certain times of the year may play an important regulatory role in bird populations (Ripple *et al.* 2013). Such predation and regulation has both positive and negative impacts, primarily related to human interests. Coyote impact on game bird populations is viewed negatively when hunting bags are reduced with low bird populations (Ripple *et al.* 2013) or coyotes consume birds of conservation value (Cooper *et al.* 2015; Dinkins *et al.* 2016). In contrast, coyote regulation of seed eating birds in agricultural landscapes benefits crop farmers (Gabrey *et al.* 1993). Predation on birds by black-backed jackals is predominantly opportunistic and it is unlikely that this predation will have population regulatory effects for birds. However, the presence of black-backed jackals in areas where endangered ground-nesting birds live could have conservation repercussions.

Dingoes and coyotes are important predators of larger prey species (Davis *et al.* 2015; Benson *et al.* 2017). In the case of the coyote, their regulatory impact on larger prey species becomes more apparent following the relaxation of regulation by apex predators (Berger and Conner 2008). Following apex predator extirpation, coyote abundance often increases and predation pressure on the juveniles of some larger prey species (i.e. pronghorn *Antiocapra americana* and dall sheep *Ovis dalli*) increases (Berger and Conner 2008; Prugh and Arthur 2015). In Australia, dingoes regulate and limit populations of larger prey such as red kangaroos *Macropus rufus* and emus *Dromaius novaehollandiae* (Pople *et al.* 2000). It is likely that in the absence of top-down extrinsic regulation, black-backed jackal impacts mirror those of the other medium canids, although the hunting strategy of black-backed jackals (preference for hider species) may lower the relative impacts in comparison to dingo and coyote that may not be limited to hider species. All four canid species are important livestock predators. Not only do dingoes have a direct effect on livestock through predation, but down-stream impacts include reduced grazing of livestock where dingoes are abundant, which has financial implications for agricultural activities (Letnic *et al.* 2012). Furthermore, the commercial cropping of kangaroos is not viable in areas where dingoes occur (Letnic *et al.* 2012). Black-backed jackals similarly play an important role in livestock predation (Kamler *et al.* 2012a; Humphries *et al.* 2016). At high jackal densities, even limited predation may have significant consequences for livestock farmers.

Indirect ecosystem effects: In the position of apex predators, medium-sized canids can suppress smaller predators and modulate their impacts on sympatric biodiversity. Dingoes and coyotes in particular have considerable impacts on sympatric mesopredators. Dingoes suppress red fox and feral cat populations via direct killing, competition for resources, and through the ecology of fear (Letnic *et al.* 2012). The consequences are that the presence of dingoes buffers smaller prey species from predation by mesopredators (Letnic *et al.* 2012; Ritchie *et al.* 2012). Lethal control of coyotes is suggested to increase raven *Corvus corax* nest predation on ground-dwelling birds (Dinkins *et al.* 2016) and mesopredator rearrangement following coyote extirpation can have severe impacts on lower trophic levels (Crooks and Soulé 1999; Henke and Bryant 1999). Red foxes, although being suppressed by dingoes in Australia (Letnic *et al.* 2011), exert their own impacts on smaller Fennoscandian mesopredator species including American mink *Neovison vison* and dampen the impact of mink on small mammals and birds (Carlsson *et al.* 2010). Thus, black-backed jackal impacts on smaller mesopredators are likely to be similar to those of other canid species, with similar cascading or modulating effects through the ecosystem likely to occur.

The top-down effects of medium-sized canids have further cascading impacts on ecosystems. The presence of dingoes permeates to an impact on vegetation - grazing by kangaroos was higher, and grass cover was lower, where dingoes were absent (Wallach *et al.* 2010). Across Australia, the presence and absence of dingoes and red foxes have cascading impacts on seed predators and therefore shrub cover (Gordon *et al.* 2017). This knock-on impact has not been investigated for black-backed jackals and it remains to be seen whether their top-down predatory effects are strong enough to generate landscape scale trophic cascades.

Ecosystem services: Coyotes, golden jackals and red foxes all consume fruits when seasonally available (Dell'Arte *et al.* 2007; Melville *et al.* 2015), thus they all play a role in seed dispersal. Canid mesopredators will readily consume carrion, undoubtedly providing a key ecosystem service by removing animal waste from ecosystems. Recent estimates suggest that golden jackals can remove up to 13000 t of animal waste across Europe, amounting to an estimated value of 2 million € per year (Ćirović *et al.* 2016). Similarly, red foxes scavenge and readily accept human-derived food (Leckie *et al.* 1998; Contesse *et al.* 2004). Medium sized canids may also influence the spread of diseases through complex interactions with their prey and sympatric mesopredators (Levi *et al.* 2012). It is unknown if, and how, black-backed jackals disperse seeds. The relative impact of black-backed jackals as waste removal agents may be dependent on the presence and density of larger obligate scavengers that limit black-backed jackal access to carrion.

Conservation-related roles – Medium sized canids have considerable conservation related roles. Coyotes hybridise with both domestic canids and canids of conservation concern (Lehman *et al.* 1991). This hybridisation has been particularly problematic in conservation efforts aimed at restoring red wolf *Canis lupus rufus* populations (Adams *et al.* 2003). In addition, domestic dogs have introgressed with other canids including coyotes, wolves and dingoes (von Holdt *et al.* 2016). Recently, hybridisation between golden jackal and domestic dogs has been recorded (Galov *et al.* 2015). Thus, although limited evidence exists of hybridisation between black-backed jackal and domestic dogs, this eventuality cannot be ruled out. Finally, since many medium sized canids have varied diets and exhibit plastic selection patterns based on prey availability, they may hamper the restoration efforts directed at rare and endangered species (Matchett *et al.* 2013). Since black-backed jackals have similarly varied diets and an opportunistic foraging strategy, they might limit the recovery of threatened species.

Role of caracal in ecosystems

Relatively little has been published on the ecology of caracal (16 kg: average weight - taken from Wallach *et al.* 2015), with virtually no studies of their ecological importance (du Plessis 2013). Through their interactions with other predators and / or with prey, however, they most likely play an important role across the spectrum of ecosystem types in which they occur (du Plessis 2013). From a biodiversity perspective, caracals potentially influence the structure of communities, regulate prey populations, and maintain biodiversity via the suppression of competing predators and prey populations, although much of this still remains un-investigated.

The presence of caracals on the landscape influences the ecology and abundance of sympatric carnivores. Caracal abundance fluctuates inversely with black-backed jackal where these species occur sympatrically (Pringle and Pringle 1979; Ferreira 1988). However, since black-backed jackals have a negative impact on smaller mesopredators, this inverse relationship may suggest that caracal presence may result in a positive effect on the abundance of smaller carnivores. However, track counts in the Kalahari show that when caracal and black-backed jackal numbers are reduced, through predator control measures, the abundance of smaller mesopredators increases (Blaum *et al.* 2009). Furthermore, caracals regularly prey on smaller predators (see chapter 7, Palmer and Fairall 1988) suggesting broad scale impacts on the abundance of sympatric mesopredators. Caracals also share a prey base with many syntopic small carnivores (Bothma *et al.* 1984; Avenant and Nel 1997; Kok and Nel 2004; Pohl 2015) thus increasing interspecific competition for available resources and the likelihood of resource-based competitive exclusion.

Few studies have been conducted on the relationship between caracal and their prey (n = 2 studies, Moolman 1986; Avenant and Nel 2002). In farming areas, caracal are considered important predators for controlling populations of small mammals (Pringle and Pringle 1979). These early observations along with numerous diet estimates provide evidence of the potential impact that caracals have on prey species. Caracals regularly consume small mammals weighing up to 10 kg, including rock hyrax *Procavia capensis*, springhares *Pedetes capensis*, rodents (mice, gerbils and molerats) (Avenant and Nel 1997; Avenant and Nel 2002; Melville *et al.* 2004; Braczkowski *et al.* 2012; Moon and Blackman 2014; Pohl 2015) and could possibly play a role in ensuring healthy prey populations and a high diversity of small mammal and bird species. Many caracal prey species consume large amounts of plant material and are known to damage natural vegetation and crops, especially where these species occur at high densities (Korn and Korn 1989; Swanepoel *et al.* 2017). Estimations from the Karoo National Park suggest that caracals have a major impact on rock hyrax populations, removing as much as 30% of the annual recruitment (Palmer and Fairall 1988). By killing small prey species it is possible that caracals impact plant communities and may be important ecosystem engineers (Ramesh *et al.* 2016), but this needs further investigation. The subterranean nesting behaviour of many caracal prey species may increase the risk of damage to farming equipment (e.g. vehicles) when their population densities, and, consequently, their burrow densities increase (S. Hanekom 1990 pers. comm.; N. Avenant 2012 pers. comm.).

Caracal kill both adult and juvenile ungulates (Avenant and Nel 2002; Pohl 2015). However, whether this predation plays a regulating role on these prey populations is unknown. Free ranging goats avoid caracal cues, indicating that caracal presence on the landscape creates a landscape of fear (Shrader *et al.* 2008). It remains to be seen what population level impact this landscape of fear creates and whether the same population level responses, as observed in northern temperate regions, emerge (Creel and Christianson 2008). Although caracals seldom scavenge, instances of caracals scavenging have been reported (Avenant 1993; Avenant and Nel 2002; Drouilly et al. in Prep) and consequently they are responsible for waste removal from ecosystems, however, not to the same effect as obligate scavengers.

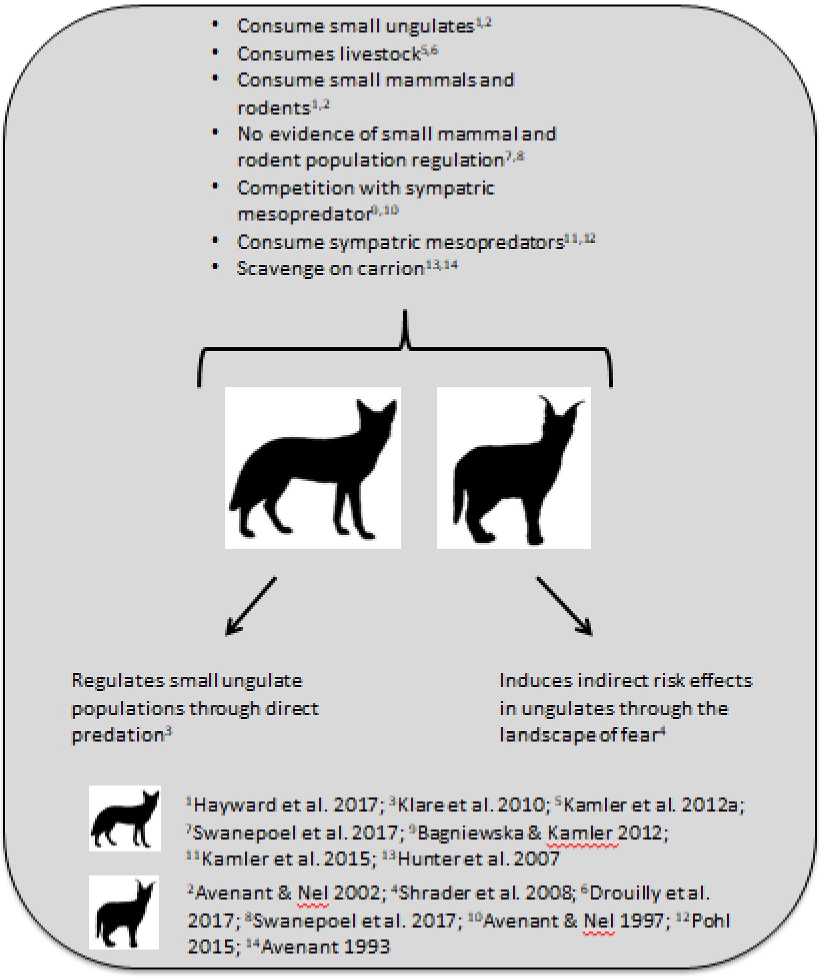

Figure 8.2: Summary of the ecological roles of black-backed jackal and caracal in South Africa based on published information (not all publications included).

<u>Using lynx and bobcat to highlight other possible ecological roles of caracal</u>

Much like black-backed jackals, our understanding of caracals' roles across ecosystems is limited. We therefore investigated other similarly-sized felids from across the globe to infer possible additional ecosystem roles for caracals. In particular, we focused on lynx (Eurasian – 23 kg, Iberian – 11 kg and Canada – 10.1 kg) and bobcats (8.6 kg; weights represent average weights taken from Wallach *et al.* 2015).

Eurasian lynx *Lynx lynx*, the largest of the four surrogate species, was the only felid investigated that regulated ungulate prey (roe deer *Capreolus capreolus*) (Jedrzejewska *et al.* 1997; Davis *et al.* 2016). Furthermore, the presence and hunting strategy of lynx influenced the habitat use (Lone *et al.* 2017), vigilance levels (Eccard *et al.* 2017) and visitation rates to feeding sites (Wikenros *et al.* 2015) of roe deer. For medium to large cervids (red deer *Cervus elephus* [120-240 kg], woodland caribou *Rangifer tarandus* [113-318 kg] and white tailed deer *Odocoileus virginianus* [45-68 kg]), juveniles are the predominant age-class killed by these felids, whereas, Eurasian lynx kill predominantly adults of the smaller roe deer [10-35 kg] (Mejlgaard *et al.* 2013; Williams and Gregonis 2015; Heurich *et al.* 2016; Mahoney *et al.* 2016). However, in the case of both the Eurasian and Canada lynx, yearlings and sub-adult lynx show greater flexibility in their diets, often selecting prey not utilised by adult lynx to avoid competition with adults for preferred prey (Mejlgaard *et al.* 2013; Burstahler *et al.* 2016). Although ungulates are consumed by caracals, we do not know whether this predation has the same regulating role as observed for Eurasian lynx and their main ungulate prey.

Like caracals, all four felid species include small mammals in their diet, with the three smaller species preying predominantly on small mammals. Canada lynx *Lynx Canadensis* and Iberian lynx *Lynx pardinus* prey heavily on lagomorphs and in the case of Canada lynx their association with snowshoe hares *Lepus americanus* may drive the observed 9-10 year lynx-snowshoe hare cycles (Krebs *et al.* 2014). Importantly, Iberian lynx are reliant on European wild rabbits *Oryctolagus cuniculus*, and declines in this food source are postulated as a key driver for the precipitous decline of Iberian lynx (López-Bao *et al.* 2010). However, despite the importance of European wild rabbits in their diet, the presence of lynx has a positive effect on rabbit abundance by regulating populations of Egyptian mongoose *Herpestes ichneumon* (Palomares *et al.* 1995 - see below), a specialist rabbit predator. Caracals similarly consume small mammals, however it is not known if this predation is regulative or whether abiotic factors may be more important for the regulation of small mammal prey. Understanding the top-down and bottom-up processes governing prey species will provide a better understanding of the possible cascading roles that caracal extirpation or hyper-abundance may provide.

The four surrogate felid species, like caracals, have important interactions with sympatric carnivores. This impact, however, varies between species and is greatest for the largest species, Eurasian lynx, which is typically described as an apex predator. The Eurasian lynx is an important predator, providing carrion for scavengers like wolverine *Gulo gulo* (Khalil *et al.* 2014; Mattisson *et al.* 2014) and red foxes (Helldin and Danielsson 2007). Despite providing food for red foxes, Eurasian lynx have a direct negative impact on red fox abundance (Pasanen-Mortensen *et al.* 2013) through direct intra-guild predation which is additive to natural mortality (Helldin *et al.* 2006). Both Iberian lynx and bobcats influence red fox activity patterns (Penteriani *et al.* 2013; Lesmeister *et al.* 2015). Bobcats, however, occur sympatrically with numerous smaller mesopredators whose space use is influenced more by habitat variables than bobcat presence (Lesmeister *et al.* 2015). Furthermore, some smaller omnivores like opossums obtain seasonal food supplementation from bobcat scats through coprophagy (Livingston *et al.* 2005). Although we know that caracals may have negative impacts on smaller mesopredators, we do not fully understand the mechanisms of these interactions.

Interactions of these four felid species on agricultural landscapes are complex and often context-dependent. Canada lynx are seldom implicated in livestock predation (Mumma *et al.* 2014) and Iberian lynx have only recently started to impact livestock (predominantly poultry but some sheep) as their abundance increases (Garrote *et al.* 2013). Most of our understanding of lynx-livestock interactions comes from Eurasian lynx in Europe. Livestock predation in multi-use landscapes is varied, with contrasting findings from various studies. In some regions predation on sheep is lower in areas with high roe deer densities (Odden *et al.* 2013) whereas in other regions predation was higher in areas with high roe deer densities (Stahl *et al.* 2002). Predation on sheep peaked in summer (Gervasi *et al.* 2014) when roe deer are not thermally or nutritionally stressed (Lone *et al.* 2017). Where sheep densities are low, female lynx seldom kill sheep irrespective of roe deer density whereas predation on sheep by males was generally higher at high roe deer densities (Odden *et al.* 2013). Furthermore, female lynx with new-born young often avoid human activity, even if high levels of prey are available near human settlements (Bunnefeld *et al.* 2006). In general, lynx were more likely to kill sheep when pastures were close to intact forest fragments, far from human settlements, associated with a high availability of roe deer and near to a pasture where livestock were previously attacked (Stahl *et al.* 2002). Lynx predation can be explained by a predictable set of habitat features that exposed sheep on certain pastures to increased risk (Stahl *et al.* 2002). Developing an understanding of the interaction between local wild prey and livestock may assist in understanding the relative impact that caracals could have on livestock and wild prey populations.

Biodiversity implications of mesopredator removal

It is clear that mesopredators are vital for ecosystem functioning and biodiversity. The global trend that the majority of research effort and funding is directed at charismatic apex predators holds true for South Africa. Furthermore, not only is the bulk of scientific inquiry aimed at this small subset of large predators (albeit those with a large ecological impact), but the majority of the research is also focused in a few select ecosystems. Moreover, until recent technological advancement in research tools, research on mesopredators was hindered by logistical constraints preventing widespread inquiry on these species. This chapter has highlighted the multitude of ecological roles that mesopredators play, however, our general understanding of these roles for black-backed jackals and caracals is limited.

Both black-backed jackals and caracals are important predators of small mammals; however understanding the regulatory or population level impacts of predation by these mesopredators remains limited. Furthermore, jackals are important predators and regulators of small- to medium-sized ungulates through the selective predation of neonates that hide. In contrast, the regulatory role of caracals on ungulate populations remains un-investigated. The predatory impact of these mesopredators varies depending on prey size and life history characteristics. Unfortunately, we need a better understanding of how these mesopredators regulate prey from the prey's perspective, rather than through more diet estimates and this should be a priority for understanding the repercussions of mesopredator management. Furthermore, the relative roles of apex predators (and their identity) on the regulatory ability of these species requires further investigation.

Through understanding important prey population responses to predation by black-backed jackals and caracals we will also increase our understanding of whether or not the presence of these mesopredators influences vegetation at a landscape scale. However, South Africa is characterised as semi-arid to arid with fairly low productivity. Research suggests that under this scenario biodiversity is more likely to be controlled by bottom-up than top-down mechanisms. However, both mesopredator species also occur in the more productive eastern regions of South Africa, and it is in these habitats that few studies have been conducted. Therefore, unravelling the main nutrient flows (i.e. contrasting bottom-up and top-down factors) across ecosystem gradients (of which basic data in many of these ecosystems remains lacking) will provide a good basis on which to formulate an estimate of the potential impacts of black-backed jackal and caracal extirpation or hyper-abundance. However, in contrast to the productivity theory, the extirpation or hyper-abundance of mesopredators from relatively simple agricultural ecosystems could have profound ecosystem impacts that may be dampened in more complex habitats with less linear food webs.

Importantly, both black-backed jackals and caracals mirror observations on other medium sized mesopredators in that they have strong top down effects on smaller mesopredators. In many ecosystems, these regulative effects have knock-on consequences for lower trophic levels and ecosystem structure. This possible ripple effect through ecosystems in South Africa through the presence or absence of these mesopredators has not been studied.

Much of what we know about the removal of these mesopredators from agri-pastoral landscapes comes from inference rather than rigorous inquiry. However, based on the above discussion, removing black-backed jackals and caracals from simple agri-pastoral environments could result in a greater abundance of small mammals (i.e. rodents) that could limit shrub regeneration through seed predation. The loss of black-backed jackals could result in small ungulate numbers increasing with a resulting increase in livestock-wild ungulate competition. However, under this scenario, the remaining black-backed jackals and caracals would have abundant prey, potentially reducing predation on livestock where wild prey are still preferentially caught (but see ideas about compensatory reproduction in chapter 5). The loss of black-backed jackals and caracals may result in an increase in population densities of bat-eared foxes, Cape foxes *Vulpes chama*, black-footed cats, African wild cats, genet species and many mongoose species, but may also lead to differences in their relative abundances (and subsequent losses of prey species of these specialized predators) in certain habitats. These populations may flourish if rodent numbers are high. In other ecosystems, smaller mesopredators have profound impacts on biodiversity and the same might be expected in South Africa. Unfortunately, our understanding of the roles of smaller mesopredators is even less than for black-backed jackals and caracals, and the resulting predator re-arrangement could alter entire small mammal assemblages, resulting in ecosystem scale consequences similar to those observed in simple island ecosystems.

<u>Glossary (Will be included in the global glossary)</u>

mesopredator, niche, guild, sympatric, mesopredator release, top-down regulation, apex predator, cascading effect, resource-driven competitive exclusion, ecosystem, latrine, metabolic scaling, hider species strategy, follower species strategy, hyper-abundant

Box 1: Key questions for increasing our understanding of the role of black-backed jackal and caracal in ecosystems in South Africa

- How does the presence or absence of apex predators (including jackal and caracal when filling the role of top predators) influence black-backed jackal and caracal density (and are these influences density dependent)?
- Do black-backed jackals and caracals regulate the populations of small ungulates (i.e. steenbok) and / or rodents (rats and mice) and / or lagomorphs (rabbits and hares); or alternatively, are ungulate and rodent populations regulated through bottom-up forces?
- If caracal and black-backed jackal prey populations increase rapidly, do these species then have negative (direct and / or indirect) impacts on biodiversity (all wildlife) – especially if sheep are protected?
- In small stock areas do black-backed jackal and caracal still distinguish between natural and domestic prey and how does the abundance of “natural” and “domestic” prey influence prey selection of these mesopredators?
- Are there landscape scale trophic cascades resulting from the localised removal of mesopredators as seen in Australia?

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