

Livestock Predation and its Management in South Africa: A Scientific Assessment

Editors

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BIOLOGY AND ECOLOGY OF THE BLACK-BACKED JACKAL AND THE CARACAL

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INTRODUCTION

Globally, several carnivore species have been implicated as livestock predators, these ranging in body size from the mongoose (Herpestidae) (e.g. Minnie, 2009) to the tiger *Panthera tigris* (Gusset, Swarner, Mponwane, Keletile & McNutt, 2009; Van der Merwe, Avenant & Lues, 2009a) and bears (e.g. Li, Buzzard, Chen & Jiang, 2013). However, medium-sized canids and felids are most often implicated in livestock predation. For example, red foxes *Vulpes vulpes* – the most widely distributed canid species apart from domestic dogs *Canis lupus familiaris* – attack and kill livestock both in their natural and introduced ranges (Sillero-Zubiri, Hoffmann & MacDonald, 2004); coyotes *Canis latrans* and dingoes *Canis lupus dingo* are the dominant predators of livestock in North America and Australia, respectively (Sillero-Zubiri et al., 2004). In addition, golden jackals *Canis aureus* prey on livestock in Africa, Europe and the Middle East (e.g. Yom-Tov, Ashkenazi & Viner, 1995). Furthermore, the Eurasian lynx *Lynx lynx* and to a lesser extent bobcats *Lynx rufus* have been implicated in livestock predation in Europe and North America, respectively (see Inskip & Zimmermann, 2009 for review). In contrast to the Canidae, the larger species of the Felidae (e.g. leopard, *Panthera pardus*) are more often implicated as livestock predators, apart from caracal *Caracal caracal* and Eurasian lynx (Inskip & Zimmermann, 2009).

In the southern African context, mesopredators – most notably black-backed jackals *Canis mesomelas* and caracal – are claimed to be the dominant predators of livestock (predominantly sheep and goats and to a lesser extent cattle) and valued wildlife species (van Niekerk, 2010; Chapter 3). Several reasons for the relatively large impact of mesopredators on the livestock industry have been suggested (e.g. mesopredator

release; see Chapter 8). However, livestock predation by black-backed jackal and caracal is probably rooted in their ethological and ecological plasticity, which allows them to persist despite centuries of population reduction efforts (Minnie, Gaylard & Kerley, 2016a; Chapter 2). This, in turn, has exacerbated their impacts on the livestock industry.

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In South Africa, humans have been relatively unsuccessful in eliminating the livestock losses caused by black-backed jackals and caracals, despite >350 years of lethal management (Kerley *et al.*, 2017). This may be due to the fact that predation management focuses on reducing mesopredator population size and does not take the ecology and biology of the target predator into account, and may thus produce unexpected population responses (e.g. compensatory reproduction). The effective management of any animal population requires a basic understanding of its biology and ecology (e.g. Knowlton, Gese & Jaeger, 1999) to assist in predicting the responses of these populations to suggested/implemented management plans (Hone, Duncan & Forsyth, 2010; Du Plessis, 2013; Chapter 6).

Developing effective management regimes aimed at reducing predation requires an understanding as to why carnivores attack livestock. Achieving this requires an understanding of the aspects of the carnivores' environment, biology and ecology that predispose them to livestock predation (Breck, 2004). A recent review indicated that there is a general paucity of information regarding the biology and ecology of black-backed jackals and caracals in southern Africa (du Plessis, Avenant & De Waal, 2015). In addition, the existing information is spatially biased, focusing on a subset of South African biomes, and predominantly derived from studies on nature reserves (du Plessis *et*

al., 2015). The dynamic nature of both black-backed jackals and caracals make generalisations across habitats and land uses difficult. This chapter synthesises the available knowledge of black-backed jackal and caracal ecology and biology, and identifies research gaps and opportunities. Additionally, where information is lacking, we make reference to ecological surrogates (e.g. coyote for black-backed jackal, and lynx species for caracal) to highlight the importance of basic biological and ecological research as it relates to adaptive management.

DIET

Resource acquisition plays a fundamental role in influencing carnivore growth, maintenance and reproduction (Fuller & Sievert, 2001). Various factors influence the ability of carnivores to obtain appropriate resources to sustain these vital processes, including inter- and intraspecific competition (Leo, Reading & Letnic, 2015), local environmental conditions (Sacks, 2005), and availability, abundance and dispersion of resources (Todd & Keith, 1983; Klare, Kamler, Stenkewitz & MacDonald, 2010). In addition, anthropogenic habitat modifications such as habitat reduction and fragmentation, as well as predator management (lethal and non-lethal) may further augment the functional responses of carnivore diets to local environmental conditions (Benson, Mahoney & Patterson, 2015). The

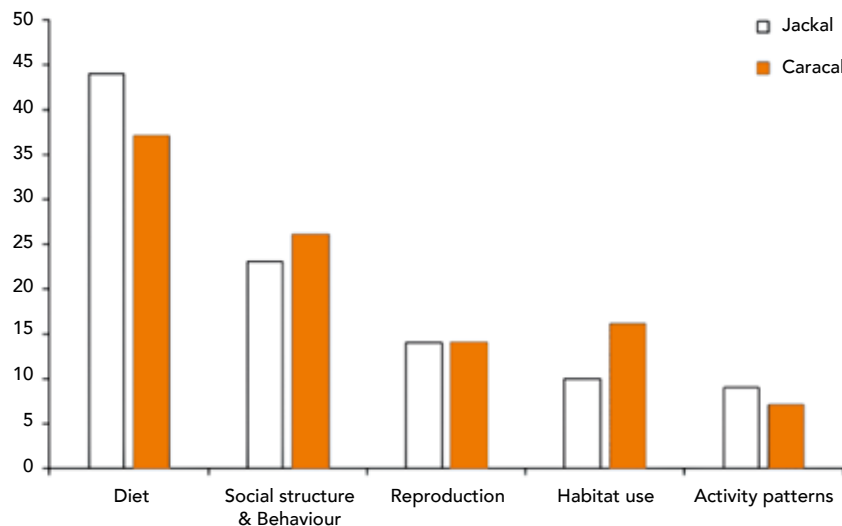


Figure 7.1. The proportion of research (peer-reviewed publications, theses and dissertations) conducted on the biology and ecology of black-backed jackals (n = 58) and caracals (n = 29) between 1960 and 2013 (adapted from du Plessis *et al.*, 2015).

diet of black-backed jackals and caracals is the most widely studied part of their biology and ecology (Figure 7.1), which is not surprising given their role as livestock predators.

Black-backed jackal

Until recently (see prey selection below), black-backed jackals, like other small- to medium-sized canids (e.g. dingo, Allen & Leung, 2014; coyote, Murray *et al.*, 2015), were considered generalist omnivores, with a catholic diet that varies according to local food availability (Loveridge & MacDonald, 2003; Kok & Nel, 2004; Fourie, Tambling, Gaylard & Kerley, 2015). The diet is dominated by small- to medium-sized mammals, and is often supplemented with birds, reptiles, carrion, invertebrates and fruit (Brassine & Parker, 2012; Kamler, Klare & MacDonald, 2012a; Morwe, 2013; van de Ven, Tambling & Kerley, 2013; Minnie, 2016). Hayward *et al.*, (2017) reported that black-backed jackals may have evolved to optimally prey on small- and medium-sized mammals. This is substantiated by the predominance of small- and medium-sized mammals in their diet, irrespective of location and season (Kaunda & Skinner, 2003; Brassine, 2011; Morwe, 2013; van de Ven *et al.*, 2013).

However, when small- and medium- size mammals become rare, black-backed jackals, like other canids, may consume a wider variety of food items (i.e. wider niche breadth) to maintain energy intake (Kaunda & Skinner, 2003). This has also been documented in coyotes (Gese, Ruff & Crabtree, 1996) and dingoes (Corbett & Newsome, 1987); when carcass availability was reduced, subordinate individuals were out-competed by dominant individuals and were forced to prey on small mammals. Additionally, black-backed jackals have been shown to prey extensively on the young of hider species (i.e. neonates hidden in the vegetation; Klare *et al.*, 2010). This results in seasonal fluctuations in the consumption of ungulate species, with neonates of hider species being consumed more in the lambing season (Klare *et al.*, 2010; Morwe, 2013). Therefore, black-backed jackals have the ability to modify their diet in response to variations in resource availability. Opportunistic feeding and dietary flexibility, amongst other factors, are suggested as causative factors in the persistence of black-backed jackal populations despite concerted



Black-backed jackal *Canis mesomelas*. Photo: Colin Grenfell.

population reduction efforts (Grafton, 1965).

Atkinson, Rhodes, Macdonald & Anderson (2002) found that black-backed jackals follow an optimal foraging pattern which allows them to opportunistically access spatially and temporally variable resources. Black-backed jackals are cursorial predators and during foraging, they typically consume the first food source encountered (Kok & Nel, 2004). Additionally, they may also access larger prey species by predation on their neonates, or this may be facilitated by group hunting and also by scavenging from apex predator kills (see resource provisioning by apex predators below). Black-backed jackals generally hunt singularly or in pairs, but may occasionally hunt in groups to improve the prospects of capturing larger prey (Moehlman, 1987; McKenzie, 1990). For example, black-backed jackals in Botswana formed temporary “packs” of six to 12 individuals to attack and kill an adult impala (McKenzie, 1990); and in Namibia they displayed similar co-operative hunting to kill an adult springbok *Antidorcas marsupialis* (Krofel, 2008).

Given their opportunistic feeding behaviour, black-backed jackals, like other canids, show intraspecific variation in diet in accordance with local resource abundance and dispersion (Macdonald & Sillero-Zubiri, 2004; Drouilly, Nattrass & O’Riain, 2018). For example, the diet of black-backed jackals on reserves in arid and semi-arid areas is dominated by small antelope (Brassine, 2011; Kamler *et al.*, 2012a; van de Ven *et al.*, 2013; Fourie *et al.*, 2015; Minnie, 2016). Conversely, black-backed

jackal diet in more mesic areas is dominated by small mammals accompanied by an associated decrease in the consumption of antelope species (Rowe-Rowe, 1983; Kaunda & Skinner, 2003). However, few studies quantify the dietary shifts of black-backed jackals between areas with heterogeneous resource availability (*cf.* Drouilly *et al.*, 2018).

Diet shifts in black-backed jackals may occur when alternative resources are provisioned. Various factors may influence the type and amount of resources available to black-backed jackals. In South Africa, the most pertinent variation in prey occurs between various land uses. Black-backed jackal diets differ considerably between agricultural and natural habitats (Drouilly *et al.*, 2018). This may be due to dietary shifts in response to resource provisioning. Here, we contrast the diet of black-backed jackals in natural systems – which include carcass provisioning by apex predators – and livestock farms – which include livestock provisioning.

Resource provisioning by apex predators

Given the black-backed jackal's reputation as a scavenger, the influence of carcass provisioning by apex predators has been widely investigated in South Africa. However, there is disagreement as to whether the provisioning of carcasses actually influences black-backed jackal diet. Some authors suggest that this is not the case (e.g. Brassine & Parker, 2012; Yarnell *et al.*, 2013), whereas others show that black-backed jackals consume larger prey species in the presence of apex predators (e.g. van der Merwe *et al.*, 2009b; Fourie *et al.*, 2015; Minnie, 2016). This suggests that scavenging from carcasses may be context-dependent and varies according to local resources and possibly the species of apex predator involved.

The presence of apex predators may also negatively affect black-backed jackal populations through predation (*i.e.* interspecific competition), and the continuum between facilitation and competition may be related to apex predator density and the species involved. For example, at low wolf *Canis lupus* densities, smaller wolf packs leave larger portions of a kill unconsumed thereby providing more scavenging opportunities for wolverines *Gulo gulo*, with the converse holding at high wolf densities (Khalil, Pasanen-Mortensen & Elmhagen, 2014). Therefore, in reserves with low densities of apex

predators, facilitation may play a more important role than competition resulting in resource provisioning (Minnie, 2016), but this also depends on how the carnivores partition the habitat. Given the context-dependent nature of black-backed jackal foraging behaviour and the contrasting results obtained in various studies, more research is required to estimate how black-backed jackal diets vary in response to varying densities of apex predators (*i.e.* facilitation *versus* competition).

Resource provisioning by humans

The availability of livestock, especially small breeds, will undoubtedly affect black-backed jackal diets. Due to domestication, sheep and goats have lost some of their anti-predator responses (but see Shrader, Brown, Kerley & Kotler, 2008), and are managed in rangelands with limited predation refuges. Black-backed jackals, like caracals, successfully attack and kill livestock. Several dietary studies conducted on livestock farms indicate that livestock may contribute a large proportion of the diet (25 - 48%; Kamler *et al.*, 2012a), but other studies show that this is not the case (e.g. only 16% of diet; Minnie, 2016). Thus, in pastoral areas, black-backed jackals may shift their diet by including livestock, consuming relatively less indigenous small- to medium-sized ungulates (often the predominant prey on nature reserves; e.g. Minnie, 2016). However, this shift in diet is context-dependent, as several studies show that black-backed jackals on farms consume more small mammals and small ungulates than on nature reserves (Bothma, 1971a; Minnie, 2016). This suggests that black-backed jackals may prefer natural prey over livestock (Table 7.1), but this is not always the case (e.g. Central Karoo, South Africa; Drouilly *et al.*, 2018). It has been hypothesised that abundant natural prey may buffer livestock losses (Avenant & Du Plessis, 2008; Hayward *et al.*, 2017; Nattrass, Conradie, Drouilly & O'Riain, 2017). Such buffering has been documented for coyotes, where a reduction in indigenous prey led in an increase in livestock predation (Stoddart, Griffiths & Knowlton 2001). Thus, maintaining a healthy natural prey base may reduce predation on livestock, but this hypothesis has not been tested for black-backed jackals.

Table 7.1. Prey preferences of black-backed jackals, indicating if prey is significantly avoided, consumed in accordance with abundance, or significantly preferred (extracted from Hayward *et al.*, 2017). The asterisk (*) indicates estimated avoidance.

Prey species				Prey species			
	Avoided	In accordance	Preferred		Avoided	In accordance	Preferred
Aardwolf				Reedbuck, mountain			
Birds				Rodents			
Blesbok				Sable	*		
Buffalo				Small mammals			
Bushbuck				Springbok			
Bushpig				Springhare			
Duiker, common				Steenbok			
Eland				Suids			
Elephant	*			Tsessebe	*		
Gemsbok				Warthog			
Giraffe	*			Waterbuck			
Hare, Cape				Wildebeest, black			
Hares				Wildebeest, blue			
Hartebeest, red				Zebra, plains			
Impala							
Kudu				Domestic prey:			
Lagomorphs				Cattle	*		
Nyala	*			Goat	*		
Ostrich	*			Livestock			
Reedbuck, common	*			Sheep			

Prey preference

Although black-backed jackals may alter their diets in response to resource fluctuations, they do display prey preferences (Hayward *et al.*, 2017). A recent study compared the prey preferences of black-backed and golden jackals and found that black-backed jackals prefer to consume birds, common duiker *Sylvicapra grimmia*,

bushbuck *Tragelaphus scriptus* and springbok (Table 7.1), and prefer to prey on species with an average (3/4 adult female body mass) body mass of 21.7 ± 3.5 kg (range: 14 - 26 kg; Hayward *et al.*, 2017). In general, black-backed jackals prefer to prey on natural prey, whilst consuming livestock in accordance with abundance, i.e. there is no

evidence that livestock are preferred prey (Table 7.1; Hayward *et al.*, 2017).

It is worth noting that black-backed jackal dietary descriptions or analyses do not provide information on the impact on the livestock- and game farming industries,

Caracal

Caracals are generalist predators, but have a more specialized diet than black-backed jackals (Kok & Nel, 2004; Melville, Bothma & Mills, 2004; Braczkowski *et al.*, 2012; Pohl, 2015; Jansen, 2016). Although mammals dominate their diet, they may consume birds, reptiles, invertebrates, fruit and seeds, and vegetation (Palmer & Fairall, 1988; Avenant & Nel, 2002; Melville *et al.*, 2004; Braczkowski *et al.*, 2012; Jansen, 2016). Caracals predominantly prey on small- to medium-sized mammals ranging in size from rodents to ungulates (up to about 50 kg; Pohl, 2015). The prey base of caracals is similar to that of black-backed jackals (Drouilly *et al.*, 2018), suggesting that these two species may compete when they occur in sympatry (Pringle & Pringle, 1979). However, no research on resource partitioning has been conducted.

Caracals may use one of two strategies to access prey: 1) a patch selection strategy may be employed when moving directly between areas (patches) where food is abundant (Stuart, 1982 ; Avenant & Nel, 1998; Melville & Bothma, 2006), or 2) when prey abundance is relatively low, caracals may employ a random foraging strategy where they move through their range and consume food as it is encountered (Avenant & Nel 1998; van Heezik & Seddon 1998; Melville & Bothma, 2006). Caracals usually prey on the most abundant prey species (Avenant & Nel, 1997; Avenant & Nel, 2002) but, like black-backed jackals, are capable of switching prey in response to spatial and temporal fluctuations in resource abundance and dispersion, albeit to a lesser extent (Drouilly *et al.*, 2018). In the driest parts of southern Africa, caracals predominantly consume mammals (Grobler 1981; Melville *et al.*, 2004; Pohl, 2015), whereas in more mesic areas the consumption of alternate prey items, particularly birds, increases (e.g. Cape Peninsula, Western Cape Province, South Africa, Leighton, G. pers. comm.). Seasonal variation in mammalian prey consumption has also been noted for caracals, where they consumed more springbok when caracal females were lactating or provisioning kittens (Avenant & Nel,

nor do they differentiate between prey that is killed and or scavenged. This would require the identification and quantification of prey killed by black-backed jackals (Chapter 3).



Caracal *Caracal caracal*. Photo: Colin Grenfell.

1997; 1998; 2002). Further, the occurrence of sympatric carnivore remains (e.g. black-backed jackals) in caracal scats is not unusual (Palmer & Fairall, 1988; Avenant & Nel, 1997; Avenant & Nel, 2002; Melville, 2004; Braczkowski *et al.*, 2012). Melville *et al.*, (2004) ascribed the presence of carnivores in caracal diet to a low density of ungulate prey, and the prospect of intraguild predation needs to be further explored. This does, however, further highlight the opportunistic feeding by caracal.

Resource provisioning by humans

Similar to black-backed jackals, diet shifts may occur when alternative resources are provisioned. However, caracals rarely scavenge (Mills, 1984; Avenant, 1993; Nowell & Jackson, 1996), although scavenging was documented in Etosha National Park where a caracal scavenged on a springbok killed by a cheetah *Acinonyx jubatus* (Nowell & Jackson, 1996) and in the Central Karoo where caracals scavenged on sheep and a kudu (Drouilly *et al.*, 2018). Thus, in contrast to black-backed jackals, resource provisioning by apex predators appears to be of little importance. The diet of caracals differs with land use, with caracals on livestock farms supplementing their diet with livestock (Pringle & Pringle, 1979;

Skinner, 1979; Stuart, 1982; Avenant & Nel, 2002; Kok & Nel, 2004; Melville *et al.*, 2004; Drouilly *et al.*, 2018), particularly during the livestock lambing season (Pohl, 2015), or when a female caracal is lactating, or accompanied by young (Avenant, 1993; Avenant & Nel, 1998). However, despite this livestock provisioning by humans, small mammals such as lagomorphs and rock hyraxes *Procavia capensis* constitute an important part of their diet (Grobler, 1981; Melville *et al.*, 2004; Pohl, 2015; Jansen, 2016). For example, on livestock farms in the Bedford district, Eastern Cape Province, caracals fed predominantly on wild prey (Pringle & Pringle, 1979), and on the farms surrounding the West Coast National Park, Western Cape Province, predation on livestock increased when the abundance of rodents decreased (Avenant & Nel, 1997; 1998; 2002). This suggests that, as suggested for black-backed jackals, caracals prefer to prey on natural prey and abundant natural prey may buffer livestock losses.

Prey preference

Although most studies indicate that caracals prey predominantly on small- to medium-sized mammals, few studies have quantified prey consumption relative to prey availability, which is essential in estimating prey preference. Several studies have shown that caracals are non-selective, consuming the prey with the highest abundance (Moolman, 1984; Avenant & Nel, 2002). However, two localised studies indicated that caracals prefer to prey on rock hyraxes, rodents and lagomorphs (Jansen, 2016; Drouilly *et al.*, 2018), and that preference for medium-sized ungulates such as common duiker, steenbok *Raphicerus campestris* and springbok varies depending on location. Similar to black-backed jackals, caracals on farms avoided sheep and goats and preferred to prey on natural prey (Jansen, 2016), providing additional support for the hypothesis that abundant natural prey may buffer livestock losses. However, more research relating prey abundance to prey consumption is required to determine the prey preferences of caracals across South Africa.

The available dietary information on caracals indicates that they are generalist and opportunistic predators that may include livestock in their diet. However, there is some evidence that they prefer to prey on natural prey and consume relatively less livestock than black-backed

jackals (Jansen, 2016; Drouilly *et al.*, 2018). Although the diet of caracals has been studied more than any other aspect of its ecology (Figure 7.1), most studies have been conducted in protected areas (see du Plessis *et al.*, 2015 for review). Thus, more research is required to determine the diet of caracal on livestock and game farms, as well as its impact on the livestock and game ranching industries.

SOCIAL STRUCTURE AND REPRODUCTION

Black-backed jackal

Black-backed jackals have a complex social structure. In a stable social system, black-backed jackals are monogamous (Moehlman, 1987). Pair formation may increase hunting success (Lamprecht, 1978) and is critical for territorial defence and the successful rearing of pups (Moehlman, 1987). However, the social structure of black-backed jackals is flexible and may consist of family groups ranging from one to eight individuals (Rowe-Rowe, 1978; Rowe-Rowe, 1982). Family groups generally comprise a mated territorial pair and their offspring (Ferguson, Nel & de Wet, 1983; Loveridge & MacDonald, 2001). However, some groups may also contain older sub-adults that have delayed dispersal to act as helpers in raising sibling offspring (Moehlman, 1979; Rowe-Rowe, 1982; Ferguson *et al.*, 1983). This is expected to occur under conditions where food availability is high (Ferguson *et al.*, 1983). Additionally, the territorial pair may tolerate subordinate individuals on the fringes of their territories (i.e. floaters, Ferguson *et al.*, 1983) and cases have been documented where black-backed jackals allowed other mated pairs, sub-adults or juveniles into their territories (MacDonald, 1979; Rowe-Rowe, 1982; Ferguson *et al.*, 1983; Hiscocks & Perrin, 1988; McKenzie, 1990; Oosthuizen *et al.*, 1997; Loveridge & MacDonald, 2001; Loveridge & MacDonald, 2003). Such relaxation in territorial defence may occur when resources are locally abundant (see Box 7.1).

The dominant mated pair typically defends an exclusive breeding territory and prevents younger subordinates from reproducing (Loveridge & Nel, 2004). However, extra-pair reproduction has been recorded and has been attributed to anthropogenic mortality (McKenzie, 1993; Walton & Joly, 2003). Polygamy – as a mechanism to compensate for high mortality (e.g.

coyote; Kleiman & Brady, 1978) – may counter lethal management aimed at reducing black-backed jackal population size by allowing more females to reproduce to compensate for increased mortality (see Box 7.2).

Mating peaks during the winter months (Skead, 1973), but late autumn and early spring matings have also been recorded (Stuart, 1981). Gestation lasts for about two months but may extend up to 70 days (Bernard & Stuart, 1992; McKenzie, 1993; Walton & Joly, 2003). Parturition usually occurs from winter to early spring (Bothma, 1971b; Bernard & Stuart, 1992; McKenzie, 1993). Additionally, parturition at a regional level may be asynchronous, as breeding pairs may reproduce within one month of each other (Bingham & Purchase, 2002). The timing of the reproductive cycle varies spatially and temporally with local environmental conditions and food availability (Fairall 1968; Rowe-Rowe, 1978; Bernard & Stuart, 1992; McKenzie, 1993; Bingham & Purchase, 2002; Walton & Joly, 2003), as is the case for coyotes (Gese, 2005). Although an earlier onset of reproduction and an extended reproductive period has been linked to increased resource availability (Bernard & Stuart, 1992; Walton & Joly, 2003), little information on the variation in reproductive cycle in response to variation in resources between land uses is available.

Black-backed jackal females have one litter per year,

and litter size ranges between one and nine, depending on the female's body condition (Minnie *et al.*, 2016a), social status (Loveridge & Nel, 2013), and anthropogenic mortality (see Box 7.2; Minnie *et al.*, 2016a). Both parents help raise the pups, which remain in the den from August to November (Ferguson *et al.*, 1983). However, as with most aspects of black-backed jackal ecology, variation in this basic pattern occurs, as pups have been recorded in dens from January to July (Ferguson *et al.*, 1983). Pups emerge from the natal den after approximately three weeks and are weaned at eight to nine weeks of age. They start foraging with their parents at three months of age, but they remain in close proximity (ca. 2 km) to the natal den until six months of age (Ferguson *et al.*, 1983; Moehlman, 1987). It is only when they get older (ca. seven months) that immature black-backed jackals start moving longer distances (see section on Dispersal).

Black-backed jackals become sexually mature at 11 months and young black-backed jackals can either: 1) become helpers (approximately one third of the litter), which aid in the raising, provisioning and guarding of subsequent litters, or 2) disperse (approximately two-thirds of the litter) from their natal range in search of mates and territories (Ferguson *et al.*, 1983; Moehlman, 1987). Families with helpers have significantly higher offspring survivorship (Moehlman, 1979).

Box 7.1 Influence of clumped, high density resources on social structure

Local resource richness and dispersion may alter carnivore spatial organisation and social structure. This should be particularly pronounced for scavenging species. Thus, given the fact that caracals rarely scavenge (see Diet), we do not expect variation in social structure in response to high-density resources. However, as home range is partly determined by resource availability, caracal density may increase when resources are locally abundant (see Home range). However, no research on the variation in caracal social structure in response to variation in resource density has been conducted. Further research is needed to determine if increased prey availability (e.g. livestock) results in a reduction in home range size and a consequent increase in population density.

Conversely, in certain instances, black-backed jackals have displayed a collapse in their typical exclusive territorial structure, which may be driven by an increase in local resource abundance. This is exemplified by variation in territory size and group size at Cape fur seal *Arctocephalus pusillus* colonies in Namibia. Here, tremendous variation in resource abundance occurs, with very high prey densities on the coast and low prey densities inland (Jenner, Groombridge & Funk, 2011). Inland,

black-backed jackals display the normal mutually exclusive territorial structure. Jenner *et al.*, (2011) reported that black-backed jackals defend these low prey density areas to maintain exclusive space to raise offspring successfully. Consequently, black-backed jackal group size is relatively small and territory size is relatively large. In contrast, at seal colonies where local resource abundance is relatively high, this territorial structure of black-backed jackals collapses, resulting in territorial overlap (Hiscocks & Perrin, 1988), increased group size and relatively small home ranges (Jenner *et al.*, 2011; Nel, Loutit, Braby & Somers, 2013).

Therefore, a local increase in resource abundance (e.g. livestock, open carcass dumps, and large animal carcass) will likely produce similar patterns as those observed at Namibian seal colonies – i.e. increased local abundance and population densities, and reduced territory size. Increased black-backed jackal densities have been documented around waterholes, antelope carcasses (Ferguson *et al.*, 1983) and at vulture restaurants (Yarnell, Phipps, Dell, MacTavish & Scott, 2015). Similar population-level responses to anthropogenic resource subsidies have been documented for several carnivores (see Newsome *et al.*, 2015 for review). Further, this may have important consequences for predation on economically important prey such as livestock and valued wildlife species, which represent “clumped resources”. For example, Yom-Tov *et al.*, (1995) found that illegal garbage dumps around informal human settlements (which included dead poultry and livestock) resulted in an increase in golden jackal population size. This, in turn, resulted in increased local predation on cattle calves.

Caracal

Caracals display the typical solitary social structure of other felids (e.g. leopard and lynx spp.), where the territory of a male may overlap with several females (Avenant, 1993; see Home range). Thus, males and females only come together to reproduce. Only females partake in parental care and family groups thus consist of an adult female and her offspring. This structure has been reported throughout their distributional range, with little variation. This suggests that caracals, unlike black-backed jackals, do not display a flexible social structure.

Unlike black-backed jackals, caracals can reproduce throughout the year. The oestrous cycle of the female is about 14 days with the oestrous period lasting three to six days (Stuart, 1982; Bernard & Stuart, 1987). The female may mate with several males (polygamy) and mating order is determined by the body mass and age of the males (Weisbein & Mendelssohn, 1989). The gestation period ranges from 78 to 81 days (Bernard & Stuart, 1987). Parturition occurs throughout the year, but peaks (74% of births) between October and February in southern Africa (Bernard & Stuart, 1987).

The fact that caracals are reproductively active throughout the year suggests that reproduction is predominantly determined by resource availability. Females need to attain an appropriate body condition

to reproduce successfully. In environments with seasonal fluctuations in resource availability, female body condition is expected to be lower at the end of winter, resulting in peak parturition in summer (Bernard & Stuart, 1987). This may coincide with the reproductive cycle of their main prey species (see Diet). Additionally, caracals feeding on livestock, which represents an aseasonal resource, may maintain a relatively high body condition throughout the year allowing them to give birth throughout the year (Bernard & Stuart, 1987). Research on Canadian lynx *Lynx canadensis* indicate that during periods of high prey availability, young females remained in or close to their natal range where they successfully reproduced (Slough & Mowat, 1996), increasing the proportion of pregnant females in the population. If a similar case exists in caracals, the presence of livestock may result in increased densities and reproduction, which may further exacerbate livestock losses. However, no research on the reproductive response of caracals to prey base variation has been conducted.

Litter size typically ranges between one and three kittens, averaging 2.2 kittens per litter (Bernard & Stuart, 1987), although litters as large as six have been reported (Weisbein & Mendelssohn, 1989). Kittens are weaned between 15 and 24 weeks of age. Bernard & Stuart, (1987) estimated that caracals reach sexual maturity

between seven and 10 months of age, after which reproduction of the caracal, as is the case for the black-backed jackal (see Box 7.2), and thus warrants future research. It is unclear if anthropogenic mortality influences the

Box 7.2 Reproductive responses to anthropogenic mortality

The lethal management of carnivores to reduce population size and the associated livestock losses may have significant impacts on reproduction. This may result in compensatory reproduction – which is an increase in reproductive output to compensate for increased mortality – that may manifest as increased litter size, larger proportion of breeding females, increased reproductive lifespan, or a decrease in age at first reproduction.

Compensatory reproduction in caracal is unknown, but presumably can occur, as it has been reported for the Canadian lynx (Parker, Maxwell, Morton & Smith, 1983) and Eurasian lynx (Bagraade *et al.*, 2016). The higher number of kittens could lead to a rapid population recovery after population reductions. It is further argued that an increase in population densities due to compensatory breeding may result in predators feeding exclusively on livestock and introduced wildlife due to their availability (du Plessis *et al.*, 2015). However, almost no research (*cf.* Brand, 1989) on the effects of lethal management on caracal reproduction has been done. It is important to determine the reproductive responses of caracals to lethal management to determine the effectiveness of these techniques in managing livestock predation.

In canids, compensatory reproduction has been documented for red foxes (Harris & Smith, 1987; Cavallini & Santini, 1996), coyotes (Knowlton, 1972; Sterling, Conley & Conley, 1983) and side-striped jackals (*Canis adustus*; Bingham & Purchase, 2002), but not dingoes (Allen, Higginbottom, Bracks, Davies & Baxter, 2015; Allen, 2015). This has also recently been documented for black-backed jackals in South Africa in response to lethal management (Minnie *et al.*, 2016a). On livestock and game farms where black-backed jackals are lethally managed, younger individuals showed an increased pregnancy rate in conjunction with larger litters (Minnie *et al.*, 2016a). This was attributed to a release in density-dependent population regulation and social dominance (due to anthropogenic mortality) from dominant individuals, which usually prevent subordinates from reproducing. Additionally, a reduction in population density may result in an increase in resource availability for the remaining individuals, thereby allowing subordinate individuals to attain a better body condition thus facilitating reproduction (e.g. coyote; Knowlton *et al.*, 1999). This increased reproductive output may result in the rapid recovery of populations to pre-management densities, thereby negating population reduction efforts. However, these findings are based on a single study in the Karoo (Eastern and Western Cape Provinces), making generalisations across habitats difficult. More research investigating the reproductive responses of black-backed jackals in conjunction with estimates of population size pre- and post-management interventions is required.

ACTIVITY PATTERNS

Black-backed jackal

The information on black-backed jackal activity patterns is scant, with less than 10% of research focusing on this aspect (Figure 7.1; du Plessis *et al.*, 2015). Black-backed jackals may be active during any part of the day (Walton & Joly, 2003), but activity tends to peak during sunrise and sunset (i.e. crepuscular; Kaunda, 2000). For example, in Botswana, black-backed jackals were predominantly active between 17h00 and 22h00 and between 05h00 and 08h00, with peaks in activity occurring around 18h00 and 06h00 (Kaunda, 2000). Black-backed jackals in the Kgalagadi Transfrontier Park, Northern Cape Province, also showed a crepuscular activity pattern, but these peaks occurred between 17h00 and 21h00 and between 05h00 and 09h00 (Ferguson, Galpin & de Wet, 1988). The timing and onset of these activity peaks seem to vary depending on local conditions, and may be due to several factors.

It has been suggested that the activity of black-backed jackals closely follows that of their main prey species (Ferguson *et al.*, 1988; Hiscocks & Perrin, 1988; Kaunda, 2000; Walton & Joly, 2003). In the North-West Province, black-backed jackal activity closely mirrored the peak foraging time of their main rodent prey species on both farms and reserves (Ferguson *et al.*, 1988). Black-backed jackals foraging at seal colonies do not display pronounced activity peaks, as they are able to utilise the resource at any given period (Hiscocks & Perrin, 1988). However, the activity patterns of black-backed jackals are not always influenced by the activity of their main prey (e.g. Loveridge & MacDonald, 2003). Apart from a few studies in isolated locations, the activity patterns of black-backed jackals have rarely been compared to that of their prey, and this warrants further investigation. This may be particularly important in livestock farming areas, and may direct livestock management practices outside of black-backed jackal activity peaks.

Seasonal variation in activity also occurs, as black-backed jackal activity increases during the winter mating season (Ferguson, 1980). This seasonal variation in activity also corresponds to the seasonal variation in sunset and sunrise times. This is not surprising, as visual predators require sufficient ambient light to successfully capture prey. Black-backed jackals in Zimbabwe were reported

to be more active diurnally, which may be due to better light conditions for hunting and predator avoidance (Loveridge & MacDonald, 2003). Similar to coyotes (Lehner, 1976), black-backed jackals may have evolved a visual system designed for crepuscular activity. This suggests that black-backed jackals should be relatively more active during full moon when light conditions are conducive to hunting. However, Ferguson *et al.*, (1988) showed that this is not the case and ascribed this to the prey easily spotting and avoiding black-backed jackals during full moon periods. Nocturnal light conditions may have important consequences for livestock predation. Lehner (1976) suggested that during nocturnal periods of low ambient light (e.g. new moon), livestock may provide more visual cues (owing to white colouration) for coyotes than natural prey, which may lead to increased livestock predation. However, this has not been investigated for black-backed jackals.

Interspecific competition may also influence black-backed jackal activity. Apart from facilitation (see diet), apex predators (e.g. leopard) also attack and kill black-backed jackals. The intensity of facilitation and competition may affect the activity patterns of mesopredators, which in turn, may depend on the density of apex predators (Newsome *et al.*, 2017; Chapter 8). Additionally, niche partitioning between black-backed jackals and side-striped jackals exists (Loveridge & MacDonald, 2003). In most parts of South Africa, black-backed jackal and caracal are sympatric, yet little information on niche partitioning between these two species exists.

Human activities, particularly lethal management, also modify the activity patterns of black-backed jackals. In areas where black-backed jackals are heavily persecuted, they are more active at night (Rowe-Rowe, 1978; Ferguson *et al.*, 1988; Hiscocks & Perrin, 1988; Fuller, Biknevicius, Kat, Valkenburgh & Wayne, 1989). With the prevalence of call-and-shoot night hunting (Chapter 6), it is speculated that black-backed jackals may become more diurnal to avoid dangerous periods. However, more information on the responses of black-backed jackals to lethal and non-lethal management is required. This will provide valuable insights in designing effective adaptive management programmes aimed at reducing predation on livestock and valued wildlife species.

Caracal

Despite the importance of caracals as predators of livestock, little is known about their activity patterns and the factors that influence them, and only two studies have investigated this in southern Africa (Figure 7.1; du Plessis *et al.*, 2015). Caracals have been described as being mostly nocturnal, but much variation in activity patterns exists across their range (Skinner, 1979; Stuart, 1982). In the West Coast National Park, Western Cape Province, caracals were active during the night, but also during cooler winter days ($\leq 22^{\circ}\text{C}$, Avenant & Nel, 1998). Both diurnal and nocturnal activity has been reported throughout their range. In Turkey, caracals were active during the day and night except for late morning and around midnight (İlemin & Gürkan, 2010). In Yemen, caracals were more active during the day (Khorozyan, Stanton, Mohammed, Al-Ra'ıl & Pittet, 2014), while they were more active late at night and during crepuscular hours in India (Singh, Qureshi, Sankar, Krausman & Goyal, 2014). Sexual variation in activity is also evident, with males being active for longer periods and moving longer distances than females. This may be due to males having larger territories to patrol (see Home range; Avenant & Nel, 1998).

Various factors influence caracal activity patterns. Several studies have indicated that rain, moon phase and wind speed do not affect activity (Moolman, 1986; Brand, 1989; Avenant & Nel, 1998). However, it has been suggested that activity may be influenced by light intensity and temperature. For example, caracals were active for longer periods on colder nights ($< 20^{\circ}\text{C}$, Avenant & Nel, 1998). Light intensity in combination with temperature may also impact activity, as males increased diurnal activity during overcast periods when ambient temperatures were between 20 and 22°C (Avenant & Nel, 1998). Diurnal hunting has also been documented when the weather is cool and overcast (Skinner, 1979). In Israel, caracals were largely nocturnal, but displayed seasonal variation in diurnal activity, depending on temperature and the activity patterns of their prey (Weisbein & Mendelssohn, 1989).

The activity patterns of caracals may mirror the activity of their main prey, but little information on this is available. However, prey size has been shown to influence activity patterns. When caracals kill larger prey (e.g. springbok) they may feed on the carcass for a few

days (Avenant & Nel, 1998). Therefore, periods of high activity linked to foraging on smaller prey (e.g. rodents and lagomorphs) may be interspersed with periods of low activity linked to the consumption of larger prey.

Caracal activity patterns are therefore context-dependent and vary with biotic and abiotic factors. They are also likely to be impacted by the intensity of human activities, especially in areas where caracals are persecuted (Ramesh, Kalle & Downs, 2016a). This may be particularly important, as spotlight hunting is used to manage caracal populations on livestock farms (Chapter 6), and may result in increased diurnal activity.

HOME RANGE AND HABITAT SELECTION

Black-backed jackal

Home range

Home range sizes of black-backed jackals vary considerably (Table 7.2), with ranges between 1 – 30 km² being reported. For example, in KwaZulu-Natal Province, average home range size varies between 6 km² (Humphries, Ramesh, Hill & Downs, 2016) and 18 km² (Rowe-Rowe, 1982) whereas in the Kalahari, Northern Cape Province, home range size varies between 2 and 5 km². In Zimbabwe, home range size varies between 0.3 and 1.3 km² (Loveridge & MacDonald, 2001), and in Namibia this ranges between 20 and 30 km² (Hiscocks & Perrin, 1988). Variation in black-backed jackal home range size may be attributed to variation in food availability and dispersion. For example, Ferguson *et al.*, (1983) showed that in areas with high prey density (e.g. abundant small mammals) black-backed jackal home range was smaller relative to areas with low prey density (see Box 7.1).

Home range size may also vary seasonally, but is unlikely to be related to seasonal variation in resources availability (Rowe-Rowe, 1982). Seasonal variation in home range size is related to the reproductive cycle, with home ranges being larger during the mating season and smaller during the whelping season (Loveridge & MacDonald, 2001). Humphries *et al.*, (2016) also documented seasonal variation in home range size in agricultural areas in the KwaZulu-Natal Province, but this was attributed to social status and was based on a small sample size. Conversely, research on coyotes in modified

Table 7.2. Mean home range, with the number of individuals tracked in parentheses (n), of male and female black-backed jackals. Only a selection of references were used to illustrate variation in home range size between various regions and land uses. MCP: Minimum Convex Polygon; FK: Fixed Kernel.

Study area	Country	Protected area	Mean home range in km ² (n)		Method	Reference
			Male	Female		
Free State Province, Benfontein Game Farm	South Africa	No	17.75 (6)	-	MCP	Kamler, Stenkewitz, Klare, Jacobsen & Macdonald (2012b)
Gauteng Province, Suikerbosrant	South Africa	No	18.05 (2)	9.5 (5)	MCP	Ferguson <i>et al.</i> , (1983)
KwaZulu-Natal Province, Giant's Castle Game Reserve	South Africa	Yes	18.2 (10)	-	MCP	Rowe-Rowe (1982)
KwaZulu-Natal Province, Midlands	South Africa	No	11.4 (3)	5.6 (1)	FK	Humphries <i>et al.</i> , (2016)
Namib Desert Coast, Cape Cross Seal Reserve	Namibia	Yes	29.95 (2)	20 (2)	MCP	Hiscocks & Perrin (1988)
Namib Desert Coast, Cape Cross Seal Reserve	Namibia	Yes	8.6 (2)	5.5 (2)	Modified MCP	Hiscocks & Perrin (1988)
North West Province, Highveld	South Africa	No	10.6 (8)	-	MCP	Ferguson <i>et al.</i> , (1983)
Northern Cape Province, Kgalagadi Transfrontier Park	South Africa	Yes	4.32 (4)	4.41 (5)	MCP	Ferguson <i>et al.</i> , (1983)

landscapes indicates that there is no seasonal variation in their home range size (Grinder & Krausman, 2001; Gehrt, Anchor & White, 2009; Poessel, Breck & Gese, 2016).

Few studies have compared black-backed jackal home range size between nature reserves and livestock farms. However, the home range size of black-backed jackals on farmlands seems to be larger than those on reserves (Table 7.2), and this may be related to a reduction in natural prey availability on farms (Ferguson *et al.*, 1983). An alternative, but untested hypothesis, is that the home range of black-backed jackals on farms may be smaller than those on reserves, owing to the locally abundant resources (i.e. livestock provisioning). This may result in increased population densities, further exacerbating livestock losses. Thus, more research relating seasonal variation in resource abundance on different land uses to home range size is required.

Owing to the monogamous social structure of black-backed jackals, sexual variation in range size is not apparent among mated pairs, as home ranges of the individuals of a pair overlap completely (Ferguson *et al.*, 1983). Some studies report variation in range size between sexes of single adults (Humphries *et al.*, 2016), whereas other do not (Fuller *et al.*, 1989). However, there is variation in range size among social classes. For example, the home ranges of adults in the Kgalagadi Transfrontier Park, Northern Cape Province and North West Province, were smaller than those of sub-adults. In the Kgalagadi Transfrontier Park adults had an average home range of 11 km² (range: 3 - 22 km²) compared to 85 km² (range: 2 - 575 km²) in sub-adults (Ferguson *et al.*, 1983). Similarly, in farming areas in the North West Province adults had an average home range of 28 km² (range: 3 - 92 km²) compared to 133 km² (range: 1 - 841

km²) in sub-adults (Ferguson *et al.*, 1983). This may be due to subordinate individuals dispersing in search of mates and territories (see Dispersal), whereas dominant pairs are more resident (Ferguson *et al.*, 1983; Humphries *et al.*, 2016).

Home ranges of dominant mated pairs may overlap slightly (less than 10%), but in general other mated pairs are excluded (Ferguson *et al.*, 1983). However, the home ranges of subordinate individuals may overlap extensively with both other subordinates (up to 82%) and dominant pairs (Ferguson *et al.*, 1983). Similar patterns were documented in the KwaZulu-Natal Province where the territories of dominant pairs did not overlap, but there was considerable overlap with the ranges of subordinate individuals (Rowe-Rowe, 1982). Additionally, unmated adults may also show large range overlap with dominant mated pairs (Ferguson *et al.*, 1983).

In general, the home ranges of mated pairs appear to be fixed with little overlap in range with other mated pairs. However, territorial collapse (see Box 7.1) and range shifts (Kaunda, 2000) may occur. Range shifts may occur when a neighbouring pair loses its territory and the dominant pairs expand their territory into the vacant area. This has also been documented for red foxes after the removal of neighbouring groups (Baker, Funk, Harris & White, 2000). However, little information on the benefits and costs of territorial shifts or expansion is available. Removal of territorial jackal pairs through management interventions may prompt this response.

Habitat selection

Black-backed jackals have a wide habitat tolerance and occur in all biomes (Minnie *et al.*, 2016b). Comparatively little research has been conducted on habitat use and selection (Figure 7.1; du Plessis *et al.*, 2015), thus necessitating generalisations across habitats. At a local scale, black-backed jackals select habitats with sufficient food resources (Ferguson, 1980; Kaunda, 2001), shelter from the natural elements, and security from competitors (Kaunda, 2001). In Zimbabwe, black-backed jackals avoid dense vegetation, preferring open grasslands and open woodlands (Loveridge & MacDonald, 2002). This reflects the higher density of preferred prey and improved vigilance opportunities against larger predators in open habitats (Loveridge & MacDonald, 2002). Conversely, in Botswana, black-backed jackals preferred savannah and

bushveld over open grasslands, which was ascribed to the increased availability of food and shelter (Kaunda, 2001). Furthermore, in the Namib Desert – which is characterised by sparse vegetation cover and severe temperature fluctuations – black-backed jackals moved to habitats with sufficient cover against the natural elements (Dreyer & Nel, 1990). Thus, habitat use appears to be driven predominantly by resource availability and habitat structure.

Habitat selection may also be influenced by interspecific competition. For example, black-backed jackals out-compete side-striped jackals for preferred habitats (Loveridge & MacDonald, 2002). Throughout the livestock and game farming areas in South Africa, black-backed jackals and caracals occur in sympatry, and this may influence habitat selection (Ramesh, Kalle & Downs, 2016b). Anecdotal evidence from farmers indicates that black-backed jackal predation is focused on the open plains in the Karoo, in the Eastern and Western Cape provinces, which provides an effective habitat for a cursorial predator. Conversely, caracals keep to the more densely vegetated and mountainous terrain, which provides more cover for an ambush predator. Habitat partitioning between these two predators has not, however, been investigated.

Anthropogenic impacts likely also influence the habitat use and selection by black-backed jackals. It is expected that black-backed jackals should avoid habitats with high human activity (e.g. Kaunda, 2000), or use habitats providing cover for avoiding humans (e.g. golden jackal; Jaeger, Haque, Sultana & Bruggers, 2007). However, this aspect of black-backed jackal ecology has not been investigated.

Caracal

Home range

Sexual variation in home range size is evident, and has been reported in several studies (Table 7.3). Female caracals in the Karoo, Western Cape Province, had smaller home ranges (range: 12 – 27 km²) than males (48 km²; Stuart, 1982). Similarly, Moolman (1986) found that males in Mountain Zebra National Park, Eastern Cape Province, had larger home ranges (15 km²) than females (6 km²). Caracal males are larger than females thus requiring larger home ranges to obtain prey, in addition to finding multiple mates (Melville, 2004;

Table 7.3. Mean home range, with the number of individuals tracked in parentheses (n), of male and female caracals. Only a selection of references were used to illustrate variation in home range size between various regions and land uses. MCP: Minimum Convex Polygon; FK: Fixed Kernel.

Study area	Country	Protected area	Mean home range in km ² (n)		Method	Reference
			Male	Female		
Eastern Cape Province, Cradock	South Africa	No	19.1 (3)	-	-	Moolman (1986)
Eastern Cape Province, Mountain Zebra National Park	South Africa	Yes	15.2 (4)	5.5 (4)	-	Moolman (1986)
KwaZulu-Natal Province, Midlands	South Africa	No	288.47 (1)	44.31 (5)	MCP	Ramesh <i>et al.</i> , (2016a)
KwaZulu-Natal Province, Midlands	South Africa	No	243.10 (1)	40.53 (5)	FK	Ramesh <i>et al.</i> , (2016a)
North-central Namibia	Namibia	No	312.6 (3)	-	MCP	Marker & Dickman (2005)
Northern Cape Province, Kgalagadi Transfrontier Park	South Africa	Yes	308.4 (1)	-	MCP	Bothma & Le Riche (1984)
Western Cape Province	South Africa	No	48 (1)	18.2 (4)	-	Stuart (1982)
Western Cape Province, Langebaan peninsula	South Africa	Yes	26.9 (2)	7.39 (3)	MCP	Avenant & Nel (1998)
Western Cape Province, Stellenbosch	South Africa	No	483 (1)	-	MCP	Norton & Lawson (1985)

Marker & Dickman, 2005; Ramesh *et al.*, 2016a). Therefore, a single male's territory typically overlaps with that of a number of females (Moolman 1986; Avenant 1993; Stuart & Stuart, 2013). Unlike black-backed jackals, in which there is little territorial overlap, the home ranges of caracals overlap both within and between sexes (Moolman, 1986). On the west coast of South Africa, male home ranges almost completely overlapped with those of females (81 – 99%), whereas overlap between females was small (0 - 19%, Avenant & Nel, 1998). Similarly, in Mountain Zebra National Park, Eastern Cape Province, same-sex overlap in home range was small, with female ranges overlapping between 2.5 and 3% and males between 2 and 14% (Moolman, 1986). Similar patterns have been documented for the caracal throughout its distributional range (e.g. in Israel, see

Weisbein & Mendelsohn, 1989).

Variation in home range size is also linked to age and social status, with dispersing sub-adults having larger home ranges than adults. For example, a sub-adult male in the Stellenbosch area, Western Cape Province, initially ranged over 480 km², and then established a much smaller range of 6 km² (Norton & Lawson, 1985). Further, females with kittens have smaller home ranges than single adult females. For example, a female caracal reduced her home range size from 9 km² to 3 km² after parturition and maintained this smaller home range until her kittens reached four months of age (Avenant & Nel, 1998).

Caracal home range size varies according to habitat, with home ranges in arid regions being larger than those in more mesic regions (Table 7.3). In the southern

Kalahari, Northern Cape Province, the home range of an adult male was large (308 km², Bothma & Le Riche, 1984). Similarly, average home range size of males on Namibian farmlands was 316 km² (Marker & Dickman, 2005). However, in more mesic regions, home ranges are smaller. On the Langebaan peninsula, Western Cape Province, males (26 km²) and females (7 km²) had relatively small home ranges (Avenant & Nel, 1998). Similarly, male (65 km²) and female (18 km²) home ranges in the Western Cape Province were much smaller than those reported in arid regions (Norton & Lawson, 1985; Stuart & Wilson, 1988). This variation in home range size along the aridity gradient is probably related to prey availability (Avenant & Nel, 1998), as mesic areas tend to have a higher density of rodent and lagomorph prey.

Seasonal fluctuations in prey availability and dispersion may also translate into seasonal variation in home range size. For example, in Saudi Arabia, a male caracal increased its range from 270 km², during seasons with a high localised prey density, to 1116 km² during seasons with a low prey density (van Heezik & Seddon, 1998). Conversely, in the West Coast National Park, Western Cape Province, seasonal fluctuations in prey availability did not influence home range size (Avenant & Nel, 1998). Thus, home range size in caracal seems to be linked to prey availability, in addition to vegetation cover and abiotic factors (Avenant & Nel, 1998).

Additionally, the range of caracal on reserves may extend onto neighbouring farms, which may result in increased livestock predation on these farms. For example, some caracals in Mountain Zebra National Park, Eastern Cape Province, had their territories confined to the reserve, but others ranged beyond the reserve border (Moolman, 1986). It is unclear how livestock provisioning will affect caracal home range. In some areas it has been suggested that caracals prefer to prey on natural prey (see Diet), thus home ranges may be larger on livestock farms due to reduced density of preferred prey (Moolman, 1986; Marker & Dickman, 2005; Ramesh *et al.*, 2016a). However, the converse may hold if caracals prefer to prey on livestock. This increase in prey densities (i.e. livestock provisioning) may result in a reduction in home range. However, more research on the variation in range size between different land uses with varying prey bases is required.

Habitat selection

Caracals are widespread within South Africa, occurring in all habitat types (Avenant *et al.*, 2016). Similar to black-backed jackals, very little has been published on the habitat selection of the caracal (du Plessis *et al.*, 2015), necessitating generalisations across habitats. In general, the caracal shows a preference for specific habitats in an area, but there is evidence that some individuals may utilise habitats more broadly (Stuart, 1981; Stuart, 1982; Mills, 1984). Caracals are ambush predators, thus habitat selection is driven, in part, by the availability of appropriate cover (Norton & Lawson, 1985). The availability of appropriate prey also affects habitat selection (Moolman, 1986; Avenant & Nel, 1998; van Heezik & Seddon, 1998; Melville, 2004). In an agricultural landscape in the KwaZulu-Natal Province, caracals preferred modified habitats over natural grasslands and forests, which was ascribed to the relatively high availability of rodents and livestock (Ramesh *et al.*, 2016a). Similar patterns have been documented for Iberian lynx *Lynx pardinus*, which vary habitat use in accordance with the level of vegetation cover and prey availability. Iberian lynx preferred natural vegetation, but also selected olive groves and heterogeneous agricultural areas with relatively high densities of preferred prey (Gastón *et al.*, 2016).

Therefore, habitat selection by caracals, like other felids, is likely driven by the availability of suitable vegetation cover (for an ambush predator) and prey. Avenant *et al.*, (2016) suggest that, the mountainous areas may suit caracal more than the plains in the Karoo and Grassland biomes owing to increased vegetation cover. However, little information on the factors driving habitat selection is available and this requires further research. Knowledge about the factors driving habitat selection may allow for the identification of predation "hotspots". For example, Eurasian lynx attacks on livestock were concentrated on 4.5% of the total area where livestock predation occurs (Stahl, Vandel, Herrenschmidt & Migot, 2001), showing that the presence of livestock alone was not sufficient to explain habitat selection. Identifying such "hotspots" may direct livestock management to less risky areas.

DISPERSAL

Black-backed jackal

Dispersal usually occurs between one to two years of age and mainly during autumn and winter (April to September) both on farmlands and protected areas (Ferguson *et al.*, 1983). It is unclear what drives dispersal, but it may be due to intraspecific competition with dominant individuals, and the need to establish a territory, find food and a mate and reproduce (Loveridge & MacDonald, 2001; Minnie *et al.*, 2016a). Loveridge & Macdonald (2001) suggested that dispersing black-backed jackals may have one of four options depending on the local conditions: (1) stay in their natal territory as a helper; (2) move into vacant territories; (3) move into nearby territories to be incorporated into those territories' resident groups; or (4) float between their natal territory and adjacent territories.

Black-backed jackals have the ability to disperse over long distances, as dispersal in excess of 100 km has been reported across several habitat types in South Africa (Bothma, 1971b; Ferguson *et al.*, 1983; Humphries *et al.*, 2016; Minnie, Zalewski, Zalewska & Kerley, 2018). Black-backed jackals appear to have few absolute dispersal barriers, as tarred roads, railway tracks, rivers and fences (including electrified "predator-proof" fences) are frequently crossed (Ferguson *et al.*, 1983; Minnie *et al.*, 2018). However, the permeability of these potential barriers varies (Minnie *et al.*, 2018). The ability of black-backed jackals to cover large distances without being hampered by fences suggests that management aimed at reducing local population size may be counteracted by immigration from other populations (Minnie *et al.*, 2018).

In areas where hunting intensity varies across the landscape (e.g. livestock- and game farms *versus* nature reserves), black-backed jackals disperse from lightly managed or unmanaged reserves into heavily managed farms (Minnie *et al.*, 2016a; 2018). This is driven by the fact that lethal management disrupts the mutually exclusive social structure, which results in vacant territories on livestock and game farms where jackal are lethally managed. Thus, black-backed jackals disperse from high-density populations into these vacant territories (Minnie *et al.*, 2016a), this may allow the recovery of hunted populations (i.e. compensatory immigration).

The combination of compensatory immigration and reproduction (see Box 7.2) in hunted black-backed jackal populations contributes to the persistence of black-backed jackals in the face of severe persecution, and indicates that lethal control of black-backed jackal populations to reduce livestock losses is unlikely to be successful if recruitment from un-hunted areas persists (Minnie *et al.*, 2016a; 2018). However, this conclusion is based on the results from a single study and spatial replication of this research is required to determine if this pattern persists across habitats. This is likely the case as similar patterns have been documented for several lethally managed canids (e.g. coyote, Knowlton *et al.*, 1999; culpeo fox (*Pseudalopex culpaeus*), Novaro, Funes & Walker, 2005; dingo, Allen 2015; red fox, Lieury *et al.*, 2015).

Caracal

Caracals may disperse from their natal range at between nine months and two years of age (Drouilly *et al.*, unpubl. data; Serieys, L. pers. comm.) and dispersal is likely driven by intraspecific competition with dominant individuals. Sex-biased dispersal has been documented for several felids, with males dispersing over longer distances than females. This increases the likelihood of dispersing males coming into contact with livestock, resulting in male-biased livestock predation (e.g. leopard, Esterhuizen & Norton, 1985; cougar, Ross, Jalkotzy & Gunson, 1996; European lynx, Odden *et al.*, 2002). This may also be the case for caracal. Some studies have reported that caracals can disperse over long distances (> 90 km; Stuart, 1982; Norton & Lawson, 1985; Avenant & Nel, 1998). Additionally, there is a general lack of information on dispersal barriers. High or electrified fences may prevent dispersal, but it is unlikely that fences represent a putative barrier.

Similar to black-backed jackal (see Black-backed jackal dispersal), the lethal management of caracal in livestock farming areas may result in the immigration of individuals from neighbouring areas where they are not managed (e.g. nature reserves). According to Visser (1978), cited in Nowell & Jackson (1996), caracals may recolonize farming areas after extirpation. This compensatory immigration has been documented for other felids (e.g. Iberian lynx, Gaona, Ferreras & Delibes, 1998; mountain lion *Puma concolor*, Robinson

et al., 2014), but no research has been conducted on caracal. Here, we hypothesise that this may be the case. However, there is a severe lack of information on caracal dispersal and the factors that may influence it, and it is one of the least studied aspects of their biology and ecology (du Plessis *et al.*, 2015). This lack of information on dispersal and dispersal barriers hampers our ability to predict the population level responses of caracal to suggested/implemented management actions aimed at reducing predation.

POPULATION DENSITY

Accurate estimates of population density for black-backed jackals and caracals in South Africa are lacking (Avenant *et al.*, 2016; Minnie *et al.*, 2016a), though many farm and reserve managers suggest that black-backed jackal and caracal densities have increased over the last 10-15 years (Avenant & Du Plessis, 2008; Du Plessis, 2013). The population density of black-backed jackals and caracals is likely related to territory size, social structure, the number of non-territorial individuals in the population, and the population growth rate. All these factors vary in accordance with local environmental conditions and resource abundance (Loveridge & Nel, 2008) and may be augmented by anthropogenic habitat modification and predator and prey management. It is of the utmost importance to develop accurate assessment methods to estimate population densities across various land uses for both black-backed jackals and caracals. This will provide the essential baseline information required for successful adaptive management.

Black-backed jackal

Several authors have estimated local population densities via extrapolating home range size, spoor counts and mark-recapture methods. Population density varies with location and recorded densities include: 35 – 40 jackals/100 km² in the Giant's Castle Nature Reserve, uKhahlamba-Drakensberg Park, KwaZulu-Natal Province (Rowe-Rowe, 1982); 50 jackals/100 km² in the Serengeti National Park, Tanzania (Waser, 1980); 54 – 97 jackals/100 km² in Hwange National Park, Zimbabwe (Loveridge & Nel, 2013); 400 – 700 jackals/100 km² in the Tuli Game Reserve, Botswana (McKenzie, 1990). Additionally, extremely high densities (equivalent to 2200 jackals/100

km²) have been recorded at the seal colonies in Namibia – these colonies representing a highly abundant year-round resource (Hiscocks & Perrin, 1988). Although these are crude estimates, it suggests that increased resource availability is correlated with increased population size. There is no information on densities on commercial livestock farms, game farms and communal areas.

Caracal

Caracal density has been estimated for a small number of reserves by extrapolating home range size. Population density in the Mountain Zebra National Park, Eastern Cape Province, was estimated at 38 caracals/100 km² (Moolman, 1986), and in the Postberg Nature Reserve, Western Cape Province, it ranged between 23 – 47 caracals/100 km² (Avenant & Nel, 2002). No other population density estimates exist for the caracal.

CONCLUSION

One might expect that research pertaining to the biology and ecology of black-backed jackals and caracals would be substantial given their role as livestock predators. However, this is not the case. Throughout this chapter we highlighted several data deficiencies and indicated areas where research is urgently required to address predation on livestock and valued wildlife species (summarised in Box 7.3). The available research has been biased towards the feeding ecology of the two species, with comparatively little information on social behaviour, activity patterns, reproduction, home range and habitat selection, dispersal, and population densities. Additionally, research is spatially biased, focusing on a subset of biomes. Given the adaptability of these predators, research needs to be replicated across several habitats to allow for accurate predictions on variation in biology and ecology between regions.

Most research on black-backed jackals and caracals has been conducted in nature reserves, with little research emanating from commercial livestock farms, game farms and communal areas. The anthropogenic impacts (e.g. prey and predator management) vary tremendously between these land uses, which should translate into variation in the biology and ecology of both black-backed jackals and caracals. However, relatively little research comparing biological and ecological variation

between these land uses (particularly communal areas) has been conducted (see du Plessis *et al.*, 2015 for review). Further, research has focused relatively more on black-backed jackals than caracals (Figure 7.1). This is not surprising given the fact that across South Africa, black-backed jackals are the most problematic predators of livestock (Chapter 3).

The collection of baseline information on black-backed jackal and caracal biology and ecology on nature reserves, commercial livestock farms, game farms and communal areas is needed for the development of evidence-based management strategies for these areas. Without it, predator management activities will continue

to be haphazard and ineffective at reducing livestock damage. The demographic, ecological, behavioural and dietary plasticity of black-backed jackals, and to a lesser extent, caracals, are probably the main factors contributing to the persistence of these species across the South African landscape. This flexibility allows them to adjust to the current prey and predator management regimes. Thus, any management aimed at modifying black-backed jackal and caracal population densities should be grounded in a sound knowledge of their biology and ecology. If this is not the case, current management practices will continue with little success.

Box 7.3 Knowledge Gaps

The collection of appropriate baseline biological and ecological data is extremely important. Without this information the responses of predator populations to prey and predator management strategies cannot be assessed. Below we highlight the important knowledge gaps where research is required in order to address predation by black-backed jackal and caracal.

- » How much livestock and valued wildlife species do black-backed jackals and caracals kill, and what are the implications of this for the livestock and game farming industries?
- » Do increased densities of natural prey buffer livestock losses?
- » How does variation in predator management (lethal versus non-lethal) affect the social structure, activity patterns, reproduction, home range, population density, habitat selection and dispersal of these mesopredators?
- » Which tools can accurately predict the density of these mesopredators?
- » What is the population size and trend of the black-backed jackal and the caracal in South Africa?
- » Are there “hotspots” of predation where most of the attacks on livestock and valued wildlife species occur?
- » Is livestock predation a learnt behaviour resulting in a few individuals killing livestock (i.e. problem individuals), as opposed to the entire population?

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CHAPTER 7

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Predators are valued as part of South Africa's natural heritage, but are also a source of human-wildlife conflict when they place livestock at risk. Managing this conflict ultimately falls to individual livestock farmers, but their actions need to be guided by policy and legislation where broader societal interests are at stake. The complexity of the issue together with differing societal perspectives and approaches to dealing with it, results in livestock predation management being challenging and potentially controversial.

Despite livestock predation having been a societal issue for millennia, and considerable recent research focussed on the matter, the information needed to guide evidence-based policy and legislation is scattered, often challenged and, to an unknown extent, incomplete. Recognising this, the South African Department of Environmental Affairs together with the Department of Agriculture, Forestry and Fisheries, and leading livestock industry role players, commissioned a scientific assessment on livestock predation management. The assessment followed a rigorous process and was overseen by an independent group to ensure fairness. Over 60 national and international experts contributed either by compiling the relevant information or reviewing these compilations. In addition an open stakeholder review process enabled interested parties to offer their insights into the outcomes. The findings of the scientific assessment are presented in this volume.

“Livestock Predation and its Management in South Africa” represents a global first in terms of undertaking a scientific assessment on this issue. The topics covered range from history to law and ethics to ecology. This book will thus be of interest to a broad range of readers, from the layperson managing livestock to those studying this form of human wildlife conflict. Principally, this book is aimed at helping agricultural and conservation policymakers and managers to arrive at improved approaches for reducing livestock predation, while at the same time contributing to the conservation of our natural predators.

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