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Understanding the black-backed jackal

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Understanding the black-backed jackal

Abstract

This paper reviews what we know about black-backed jackal ecology, drawing implications for managing human-wildlife conflict with this species. We review the research literature on the black-backed jackals in the context of other African jackal species and with regard to its diet (part 1), its breeding, territoriality and sociality (part 2), and its role as a 'problem animal' for small stock farmers (part 3). We argue that both the historical record (see also Nattrass et al.*, 2017) and the scientific research points to the need to understand the black-backed jackal as a very adaptable animal whose diet, breeding strategies and social arrangements are context-dependent. We draw implications for the management of black-backed jackal predation (part 4) and need for further research, especially on farmlands and landscapes undergoing a transformation in land use. The paper is part of an inter-disciplinary project about sheep farming and predators in the Karoo.*

1. Black-backed jackals and the African jackal family

According to the fossil record, black-backed jackals (*Canis mesomelas*), also known as silver-backed jackals or red jackals, have roamed East and Southern Africa for 2 to 3 million years (Hendey, 1974; Savage 1978).[1] They weigh between 6.5 and 8.5 kilograms,[2] resemble foxes with their rufous brown fur, large triangular ears, bushy tail and long snout, and are distinguishable by their distinct silvery black-saddle (Figure 1). Their conservation status is 'of least concern'.

There are two other species of jackal in Africa: the side-striped jackal (*Canus adustus*) which occurs in West, central and southern Africa (Atkinson &

[1] Black-backed jackals are found in two distinct populations, one in East Africa (where they are known as *Canis mesomelas schmidti*) and the other in Southern Africa where they are known as *Canis mesomelas mesomelas* (Walton and Joly, 2003: 1; Loveridge and Nel, 2004: 163).

[2] See overview of studies in Deacon, (2010: 8) showing also that males tend to weigh more than females.

Loveridge, 2004: 152), and the 'African golden wolf' (*Canis anthus*), occurring in North and East Africa. Originally seen as a member of the golden jackal species (*Canis aureus*), recent genetic evidence suggests that the African golden wolf diverged from the Eurasian golden jackal more than a million years ago and is deserving of its own species (Koepfli *et al*., 2015).

Despite having diverged from a common ancestor two million years ago (Wayne *et al*., 1989), the various species of African jackal are morphologically similar (Koepfli *et al*., 2015) indicating that their particular size and shape was well suited to their evolutionary niche as opportunistic, mesopredators.[3]

Figure 1: A young black-backed jackal in Anysberg Nature Reserve (Western Cape Karoo).

[3] Ecological theory assumes that a successful evolutionary strategy for a carnivore is to 'choose prey carefully' so as to maximise the energy gained from food at the lowest cost in terms of energy expended and risk of injury (Schoener, 1971). Relatively small, opportunistic predators are able to exploit a wide range of options and thus can be expected to do well.

Jackals are opportunistic feeders, including a very wide range of food sources such as insects, termites, snakes, small- to medium-sized mammals, fruits, seed, spiders, other plant material, birds, reptiles, fish, eggs and carrion in their diet. Side-striped and golden jackals tolerate wetter and more densely vegetated habitats than the black-backed jackal, and are known to live on the fringes of human settlements and include human refuse in their diet (Atkinson & Loveridge, 2004: 153). They are also known to kill smaller predators like bat-eared foxes, mongooses and Cape foxes (Kamler *et al*., 2012, Kamler *et al*., 2013) presumably to reduce competition[4] and as an opportunistic food source.

Unlike the side-striped jackal, the black-backed jackal tends to shy clear of human settlements.[5] However, in Botswana there are indications that anthropogenic food sources such as rubbish dumps, domestic chickens, dogs and cats as well as refuse from fishing activities have become small but significant aspects of black-backed jackal diet (Kaunda & Skinner, 2003).

Black-backed jackals are known to dominate side-striped jackals, even though they are typically smaller than side-striped jackals. A study from the early 2000s of both species of jackal in the Hwange estate (an unfenced conservation area with some human habitation adjacent to Hwange National Park) in western Zimbabwe found that black-backed jackals mostly occupied grassland and avoided woodland whereas the side-striped jackal favoured dense vegetation and had home ranges centred on safari camps (Loveridge & Macdonald, 2003: 146). Black-backed jackals aggressively defended their grassland territory [where they were eating springhares (*Pedetes capensis*)][6] from the side-striped jackals (*ibid*: 150; Loveridge & Macdonald, 2002).[7] Human refuse occurred frequently in the scats of the side-striped jackal and rarely in the scats of the black-backed jackal (ten times less).[8] Dietary overlap was greatest in the wet season when food resources were abundant and lowest in the dry season. Loveridge & Macdonald (2002) conclude that the jackals did not have clear cut ecological niches, and

[4] Cape foxes thus avoid black-backed jackals by hunting at night and through dietary partitioning (eating more insects and fruit) whereas bat-eared foxes seek protection in larger groups and keep their den sites out of black-backed jackal territories (Kamler *et al*., 2012).

[5] An indication of the relative tolerance for contact with human settlement is that the side-striped jackal is responsible for 80 percent of recorded cases of rabies in Zimbabwe. Bingham and Purchase argue that this probably originated from contact with domestic dogs because there are no jackal-rabies cycles in national parks (1999: 551).

[6] The black-backed jackal was diurnal, being most active at dawn and dusk, and this was synchronised with springhare activity (Loveridge & Macdonald, 2003: 147).

[7] In 21 of all 23 inter-specific encounters, black-backed jackals either chased the side-striped jackal away, or the side-striped jackal retreated (Loveridge & Macdonald, 2002: 603).

[8] The consumption of springhares and arthropods varied seasonally, but not scavenged ungulates, rodents, fruit, birds and refuse (*ibid*: 149).

that extreme flexibility of diet and behaviour allowed them to co-exist sympatrically (in the same area) over part of their range.

In the Serengeti, golden jackals and black-backed jackals occupy different habitats, with implications for social organisation and breeding behaviour. Black-backed jackals have their pups in the dry season when the unstriped grass rat (*Arvicanthis niloticus*) is at peak numbers and when there are opportunities for eating fruit and berries. Moehlman argues that catching small packets of food (rodents) requires large territories and strong co-operation between bonded pairs in provisioning food for pups. The golden jackal, by contrast, raises pups in the wet season when they kill fawns of Thomson's gazelle (*Eudorcas thomsonii*) (Moehlman, 1987: 366) and scavenge afterbirths and carcasses. Their territories are smaller than the black-backed jackals and male investment (in provisioning for the pups) is less important than for the black-backed jackals (which require substantial parental investment in obtaining rodents for the pups). According to Moehlman's observations, pair bonding is thus weaker for golden jackals than black-backed jackals in the Serengeti (*ibid*: 369).

Black-backed jackals prefer relatively open habitats, a characteristic that suites their role as coursing predators (taking prey on the run) (Loveridge & Macdonald, 2003: 150). However, they are also 'searchers' (especially of young fawns hiding in the vegetation) and scavengers. Compared to the other jackal species, the black-backed jackal has a smaller molar grinding area and a larger pre-molar cutting blade, indicating that it evolved to specialise mostly on meat whereas the side-striped and golden jackals are more omnivorous, and are closer to the red fox (*Vulpes vulpes*) in this regard (van Valkenburgh, 1991: 343-4).[9] Whereas side-striped jackals are generally not known to be significant predators of livestock, black-backed jackals are a problem for farmers in many live-stock producing areas of South Africa (Loveridge & Macdonald, 2003: 144).

Black-backed jackals kill sheep (mostly lambs) by strangulation (biting on the neck to seal the trachea) which is similar to how they kill wild ungulates[10] (Rowe-Rowe, 1975: 79). In Botswana black-backed jackals have been observed hunting larger ungulates like impala (*Aepyceros melampus*) collectively on an opportunistic basis (McKenzie, 1990) and singly (Kamler *et al*., 2010). Do Linh

[9] Fossil records indicate that the carnassial length of black-backed jackals tends to increase with south latitude and modern samples indicate that skull size also increases further South (Klein, 1986: 13).

[10] Black-backed jackal kills are distinguishable from those of domestic dogs in that their kills are 'neater' whereas dogs typically tear up the carcass, sometimes not even eating it (Rowe-Rowe, 1975: 80). Domestic dogs are closer to wolves and the golden jackal in their killing methods (*loc.cit*).

San *et al*. (2009) found that one fifth of black-backed jackal diet in the Great Fish River Reserve (where there are no apex predators) comprised ungulate lambs and calves. Klare *et al*. recommend that black-backed jackals should be seen as members of the large carnivore guild given their capacity for hunting ungulates (2010: 1039).

Black-backed jackals are, however, also adept at scavenging carrion (Van de Ven *et al*., 2013) and are known to feed on carcasses around lions and spotted hyenas (Loveridge & Macdonald, 2002: 604). In Botswana, they may also have an association with particular prides, following them to scavenge on their kills (Smithers, 1971: 149). The importance of carrion in increasing black-backed jackal numbers was shown recently with the introduction (and then cessation) of a 'vulture restaurant' (the provision of dead cattle from farms) in the Mankwe Wildlife Reserve in the Northern Province. Black-backed jackal [and brown hyena (*Hyaena brunnea*)] abundance increased after the introduction of the vulture supplementary feeding program, and declined after it was ended – whereas black-backed jackal numbers remained stable in nearby Pilansberg National Park where no vulture restaurants were provided (Yarnell *et al*., 2015).[11] Ćirović *et al*. (2016) found that in Serbia, the golden jackal was important as a 'cleaner' of anthropogenic animal waste such as dead livestock and the remains of hunted animals. They argued that this, together with the fact that the golden jackal consumed large numbers of pest rodent species, implied that this mesopredator provided unacknowledged 'ecosystem services' for people in the area. They argued that as farmers in the area were not complaining about stock losses, any livestock consumed was almost certainly carrion.

In the first 'natural history' of the black-backed jackal, Fitzsimons assumed that it had evolved primarily as a scavenger but had subsequently become a specialist predator of colonial live-stock in South Africa as a consequence of the extirpation of large predators and migratory herds of game (Fitzsimons, 1919b: 97, 100). There is some support for this hypothesis in that scavenging opportunities from large ungulates killed by cheetahs (*Acinonyx jubatus*) were the predominant food source for black-backed jackals in the Samara game reserve (near Graaf Reinet in the Great Karoo, Eastern Cape) and this did not vary across seasons. However, Brassine & Parker (2012) found that black-

[11] Minnie *et al*. (2016) found from a study of culled black-backed jackals in the Eastern Cape that breeding females were better nourished than non-breeding females suggesting that the dynamic behind this increase in population is likely to have been the provision of food, rather than immigration into this fenced reserve. Similar results have been found for coyotes (*Canis latrans*) in the United States with the onset of reproduction and successful rearing of pups being positively linked to nutritional status (Knowlton *et al*., 1999: 400; Sachs, 2005; Gese, 2005).

backed jackals actively predated on ungulates, young and old, in game park areas of the Eastern Cape irrespective of whether larger carnivores (and hence scavenging opportunities) were evident. Yarnell *et al*. (2013) came to similar findings. This suggests that the balance between scavenging and active hunting varies according to context and that it is best not to draw conclusions about back-backed jackal dietary preferences in the abstract. A study of black-backed jackals on the Skeleton coast of Namibia revealed that they were unselective scavengers of dead fish, birds and penguins and actively hunted and killed seal pups (Avery *et al*., 1987), pointing once again to opportunistic hunting and scavenging behaviour.[12]

A study of the diet of black-backed jackals and brown hyenas (*Parahyaena brunnea*) in the North-west Province (in protected areas and on farms) found significant overlap between the two species, but that the black-backed jackal was more likely to hunt its prey than the hyena (van der Merwe *et al*., 2009). Black-backed jackal diet in the Namib Desert has been found to comprise mostly the giant longhorn beetle (*Acanthophorus capensis*) and locust (*Anacridium moestum*) with mammal remains found in only one third of the samples (Goldenberg *et al*., 2010). Insects were also the most common item found in a sample of black-backed jackal stomachs in Botswana, followed by small mammals and carrion (Smithers, 1971: 149-150). Such studies highlight how the diet of the black-backed jackal alters depending on locally abundant food sources. Their diet varies seasonally along with the prey base (Forbes, 2012).

A recent study of black-backed jackal diet before and after two management interventions in the Karoo National Park, namely the population reinforcement of springbok (*Antidorcas marsupialis*) and then the reintroduction of lions (*Panthera leo*), also reveals their dietary flexibility. After additional springbok had been released into the park, black-backed jackals consumed more springbok, but following the reintroduction of lions which produced scavenging opportunities on large ungulates, they consumed more large ungulate carrion and their relative consumption of springbok declined to pre-reinforcement levels (Fourie *et al*., 2016). The authors conclude that this highlights 'just how context-dependent the diet of a small generalist predator is, with rapid and substantial shifts in diet as the resource-base shifts' (2016: 8). In support of this conclusion is the findings from a nature reserve in Kwa-Zulu Natal, were black-backed jackals were found to be mostly 'searchers' (and pursuers and scavengers only

[12] Because they were so unselective, Avery *et al*. (1987) suggest that black-backed jackal middens (bone and debris piles near resting places) could potentially be used as an index for measuring changes in fish stocks or climate change on penguins.

opportunistically) and to utilise the most abundant, conveniently sized prey (Rowe-Rowe, 1983).

A study of black-backed jackals in the Cape Cross Seal Reserve on the Namib desert found that the Cape fur seal (*Arctocephalus pusillus*) was the main food item, followed by birds (mostly the cormorant) – the rest being 'unidentified vertebrates' (Hiscocks & Perrin, 1987). The study included direct observations of feeding and confirmed that most food was carrion with 36/37 cormorants eaten being scavenged (the other was a waterlogged bird) (*ibid*: 56). Black-backed jackals were seen drinking from temporary rock pools caused by fog condensation, and licking condensed moisture off rocks in addition to scraping lichen off rocks to consume (*loc cit*). They attacked dying adult seals, and pups, but otherwise ate seal carcasses that washed up on the beach *(ibid*: 57).

Studies that link black-backed jackal diet to an index of prey abundance are able to determine whether jackals 'prefer' certain prey items, that is, if they consume a greater proportion of them than their relative availability in the landscape. Kamler *et al*. (2012b) found, using scat analysis, that on a sheep farm in the Free State, 25 to 48 percent of the biomass consumed by black-backed jackals was sheep (with consumption peaking in the lambing season) and that wild ungulates such as springbok and steenbok (*Raphicerus campestris*) comprised 8 to 47 percent of the biomass. Although sheep were the main food source, compared to the biomass available, black-backed jackals selectively consumed mammals of between 1 to 3 kilograms across all seasons and wild ungulates were selectively consumed over sheep in most seasons.[13] Kok & Nel (2004) compared the dietary composition of black-backed jackals in the Free State with sympatric felids (caracal and African wild cat), finding that they had a much higher ratio of opportunistically caught prey (notably invertebrates) and that the capacity of the black-backed jackal to consume a wide variety of food sources allowed it to live sympatrically with other potentially competitive predators.

In short, the literature on black-backed jackal diet is strongly suggestive of great adaptability to local food sources and the presence of other predators. In a recent meta-analysis of dietary studies of black-backed jackals and golden jackals, Hayward *et al*. conclude that dietary preference appears to be shaped by 'top-down' factors such as the presence of large carnivores and 'bottom-up' factors such as prey size, abundance, behaviour and habitat. Their analysis of available data suggests that golden jackals have a consistent preference for hares, and

[13] Note that as this study was conducted on scat (rather than stomach contents or direct observations of feeding) it is impossible to tell how much of the mammal protein in this study was scavenged carrion.

black-backed jackals for small ungulates, mostly higher species such as springbok. However, their findings say as much (if not more) about the geographical location of the underlying studies as it does about what 'the' black-backed or golden jackal prefers.[14] We caution against making overly universalising claims about black-back jackal diet given how adaptive and flexible it has proved to be across different landscapes.

2. Breeding, territoriality and sociality

As discussed above, black-backed jackals form strong pair bonds, a factor Moehlman (1987) has attributed to the importance of male investment in pup provisioning. Ferguson *et al*. (1978) found that allogrooming (social grooming) was common amongst black-backed jackal pairs in the Kalahari Gemsbok National Park and that pair members greet each other with a fixed 'greeting' ceremony. Calling behaviour appears also to be linked to pair dynamics in that most calling takes place during the breeding season, presumably being linked to pair formation and the establishment and defence of territories (Skead, 1979).

However, the social structure of black-backed jackals appears both flexible and complex. The bonded pair forms the primary social unit (Moehlman, 1987), yet black-backed jackals have a remarkable range of visual signals and social postures' rather like the coyote (Ferguson 1978: 161). This, as discussed further below, is suggestive of a social hierarchy more often associated with a pack.

In his observational study of black-backed jackals in a nature reserve in Botswana, Kaunda (1998) found that aggressive encounters between jackals were extra-pair disputes over food and territorial boundaries,[15] but that most encounters were not aggressive, but rather entailed agonistic postures and signalling. This in turn implies a degree of broader sociality, at least to the extent that black-backed jackals understood the messages being conveyed, thereby allowing most boundary disputes to be managed without overt aggression or dangerous fighting. Understanding of this broader social 'language' also allows jackals to be facultative (i.e. opportunistic) co-operative hunters (i.e. are able to hunt co-operatively in quickly and loosely formed packs if the opportunity arises) – see further discussion below.

[14] There are also question marks about the reliability of the estimates of prey availability in some of the underlying studies.

[15] Kaunda observed aggressive interactions on 38 occasions, and none were between members of a pair. Most occurred around food (23 of the 38 encounters) or were territorial disputes (9 occasions) (1998: 133).

There is significant variation in the timing of the breeding season for black-backed jackals (Bingham & Purchase, 2002). In the Western Cape Province of South Africa and in the Transvaal, black-backed jackals have been known to produce pups in the winter[16]/spring, between July and September (Bernard & Stuart, 1992: 293; Bothma, 1971a). However, they have also been known to produce pups in the late spring and early summer in the Eastern Cape (Hall-Martin & Botha, 1980) and Botswana (Smithers 1971: 151). In the Serengeti black-backed jackals produce pups between June and November when rodents and fruiting bushes are relatively plentiful (Moehlman, 1987). The timing of the breeding season is probably related to food availability, with this also being influenced by resource partitioning behaviour in the presence of competitors. For example, the presence of golden jackals in the Serengeti may have been a factor affecting why black-backed jackals bred in the dry season (and hence were dependent on rodents) rather than in the wet season when golden jackals were taking advantage of fawns and after-births to feed their litters (Moehlman, 1987).

Studies of placental scarring reveal that litter size for black-backed jackals varies from one to eight pups with a mean of about four (Bothma, 1971a; Bingham and Purchase, 2002). Litter size amongst coyotes has been strongly correlated to food availability (Gese, 2005: 281) and this is probably also the case for black-backed jackals (Moehlman, 1979, 1987; Minnie *et al*., 2016).

Black-backed jackal pups emerge from the den after three weeks, are weaned at 8-9 weeks and by 14 weeks are well co-ordinated and starting to forage with the adults (Moehlman, 1979). They are sexually mature after 11 months and some disperse after about six months (Ferguson *et al*. 1983), others stay longer, sometimes to help with the next year's litter. Dispersal is generally thought to be driven by competition with the adults for food and hence the need to find and establish their own territories. This hypothesis is supported by evidence showing that an increase in local food availability, such as the opening of a vulture

[16] Bernard and Stuart argue that medium-sized canids, including the side-striped jackal, breed in the warm wetter weather, presumably when prey is most abundant (1992: 292) and they attribute the black-backed jackal's winter breeding behaviour to the presence of ungulate carcasses in winter. They argue that black-backed jackals are better suited to scavenging than the side-striped jackal given their relatively large carnassial teeth and robust skull (*ibid:* 293). Bingham & Purchase (2002), however, found that in Zimbabwe, for both the side-striped and the black-backed jackal parturition took place in spring (September and October). They point out that studies show that the timing of parturition varies regionally and over time, and that the Bernard and Stuart data, which drew on samples from different years and across the Western Cape, might have been confounded by such variation (2002: 25).

restaurant, results in genetically distinct clusters of black-backed jackals (James *et al*., 2016) as the benefits of dispersal fall relative to staying. In the language of ecologists, black-backed jackals are thus facultative cooperative breeders, capable of breeding as lone pairs and forming extended family groups when ecological conditions (abundant food and limited vacant territories) favour philopatry (staying in a particular, usually natal area) over dispersal.

Whether black-backed jackals live in groups or in pairs is likely to vary depending on a complex set of factors including the type of prey available, the ease of provisioning pups and the costs and benefits to juveniles of dispersal (Macdonald, 1983; Moehlman, 1987; Jenner *et al*., 2011).[17] Persecution by man might also affect group size. For example, Macdonald attributes the fact that coyotes in Texas feed mainly on rodents and live in groups, whereas coyotes in the Rocky Mountains live in pairs despite also living mainly on rodents (1983: 381), to the persecution of coyotes in the Rocky Mountains. He speculates that hunting reduces group size directly and by creating vacant territories, reduces the costs of dispersal and establishing a breeding territory (*loc.cit*).

Young black-backed jackals are known to disperse over large distances.[18] This is similar to the American red fox which has been observed to disperse in a clear directional movement that is 'efficient in terms of energy and of time spent in unfamiliar terrain, to distribute foxes throughout local areas and to find areas vacant of other foxes' (Storm *et al*., 1976: 62).[19] In South Africa, a six-month old male black-backed jackal was tagged and eight months later killed (on a

[17] In Israel, around a rubbish dump, golden jackals lived in stable groups of 10 to 20 and defended territories of less than 0.1 km^2 (Macdonald, 1979). A study of golden jackals in Ethiopia (Admasu *et al*., 2004) in and around the Bale National Park found much larger home ranges (from 8 to 65 km^2). All radio-collared animals were determined to be of the same social group. However they retained monogamous pair bonds but ranges were large and jackals tended to be solitary (suggesting that food resources were widely dispersed and rarely concentrated enough for jackals to forage in groups).

[18] Dispersal of black-backed jackals has been recorded in autumn and winter on both farmlands and protected areas (Ferguson *et al*., 1983: 497), though timing is likely to be strongly affected by when the jackal pups were born.

[19] Storm *et al*. (1976) found that dispersal distance was not related to whether the animal had been castrated (as part of a controlled experiment conducted by researchers), was not caused by overt aggression from socially dominant individuals or related to shortages of food. The foxes dispersed exclusively at night (*ibid*: 37), resting when they came against barriers, such as cities, big rivers, fences, often provoking a change of direction (*ibid*: 39). They followed clear directional movements (unless responding to an obstacle such as a river) and 'several ended their journey with a circular routes, returning to a place previously passed (*ibid*: 45-6) to establish new territories. NB, the radio-collared black-backed jackal known as Leroy (footnote 14) also dispersed at night, in winter, in a clear directional movement and ended his dispersal with a circular route.

farm) a straight line distance of 103 kilometres from the release site (Bothma, 1971c). Ferguson *et al*., (1983), recorded a young dispersing male black-backed jackal in a stock farming district of the Western Transvaal as having moved 87 kilometres over four nights to a point 45 kilometres in a direct line from the release site. It stayed in a fixed range for 5 weeks and then moved another 30 kilometres and was killed 13 months later, at a point 126 kilometres in a direct line from where it had been released. As it had crossed tar roads, railways and irrigation channels, Ferguson *et al* concluded that 'it would thus seem that few barriers limit the dispersal of the black-backed jackal' (1983: 493).[20]

2.1. Helpers at the den

Visual observations in the Serengeti (Moehlman, 1979; 1987) and Kalahari Gemsbok National Park (Ferguson *et al*., 1983) revealed that more than two adult jackals may be involved in raising pups. According to Moehlman's intense observation of fifteen litters, 'helper' jackals were pups from the previous year that stayed in their parent's home territory. Each helper added 1.5 surviving pups to the litter by catching and regurgitating food for them and protecting them when the breeding pair was away (Moehlman, 1979: 383; 1987). She observed that because helper jackals are as related (genetically) to their full siblings as they are to their own offspring, staying on as helpers and delaying their own reproduction for a year could improve their inclusive fitness[21] by facilitating the survival of close relatives (1979: 372). Remaining in their parent's territory might also assist in their own survival by giving them time to perfect their hunting skills in a familiar environment (Ferguson *et al*., 1983: 500). Ferguson *et al*., found evidence of submissive jackal 'helpers' in dens both in the Kalahari Gemsbok National Park and on farmlands (1983: 497).

Moehlman found a much stronger correlation between pup survival and the presence of helpers at the den for black-backed jackals than for golden jackals. She attributed this to the fact that black-backed jackals had larger home ranges and were more reliant on the hunting effort of individuals to catch small prey items (rodents) than the golden jackals, which as discussed above, ate larger prey items such as fawns during the breeding season (1987: 371). Jenner *et al*.

[20] A young male black-backed jackal (known as 'Leroy') who was radio-collared by Marine Drouilly in 2013 and travelled about 110 kilometres in two weeks, in direct line from his release site near Beaufort West travelling also exclusively at night. Humphries *et al*. (2016) caught an adult male black-backed jackal in the Natal midlands that dispersed over 150 kilometres during winter and spring (2016: 4).

[21] Inclusive fitness means increasing the chances that their genes will be passed on (by close relatives).

made a similar argument about the use of helpers to offset costly trade-offs (in terms of time and energy) between care of pups at the den and food acquisition away from the den (Jenner *et al*., 2011: 232). They argued that black-backed jackal group size in the Cape Cross Seal Reserve in Namibia was larger for den sites further from the seal colony because the distance to seal carcasses on the coast was longer, thus requiring more individual helpers (presumably offspring from previous litters)[22] to assist in the successful raising of a litter of pups.

Helpers typically do not breed at their natal den: they do not display sexual behaviour, leading to speculation that there is social suppression of endocrine function (Moehlman, 1987: 371) and/or incest avoidance. However, there are exceptions to a single breeding female per den. Ferguson *et al*. cite two cases where black-backed jackal pups, differing by a few weeks in age were pulled from the same natal den, suggesting that the adult breeding male had also mated with the helper who then gave birth in the same den as the adult female (1983: 499). It is, however, also possible that a female helper may have been mated by an unrelated male and given birth in her natal den. Ferguson *et al*. speculate that 'polygamy may be one of the mechanisms with which jackals compensate for high mortality' (*loc.cit*).

There is evidence that foxes and coyotes, although typically monogamous, are sometimes able to support polygamous breeding arrangements (see review in Hennessey *et al*., 2012) and this might sometimes be the case on with black-backed jackals. A professional black-backed jackal hunter told us that he had killed a breeding pair and six pups in a den on a farm and had gone back the next night and killed another female emerging from the same den with swollen teats. In his assessment, this was a helper with her own litter because the food supply on that particular farm in the South African Karoo could support a dual litter.[23] Polygamy is, however, likely to be unusual given evidence from other wild canids showing strong competition between females (over male investment in their offspring) and the active suppression of subordinate's breeding including the killing of pups (Moehlman, 1987: 373-5). Perhaps in the case cited by Ferguson *et al*. there was sufficient food available on the farmland for two litters of pups and that the black-backed jackal's social arrangements could adapt to it. It is also possible that the closeness in age of the subordinate pups to the dominant female's pups prevented infanticide.

[22] NB: Group structure in canids is usually based on long-term affiliations between a pair and matured offspring (Kleiman & Eisenberg, 1973).
[23] Interview with Andre Botha, 5 November 2014.

2.2. Territoriality

Territoriality is important in coyotes for ensuring access to food resources and functions as a social means of limiting reproduction (Knowlton *et al*., 1999; Gese, 2005). The same is likely to be true for jackals (Moehlman, 1987). Black-backed jackals have been recorded with territory sizes ranging from 2.1 km^2 to 91.5 km^2 with smaller territories generally associated with greater resource abundance (Ferguson *et al*., 1983).[24] Areas with a concentrated (or 'clumped') food supply can also support a higher density of jackals. For example, the presence of clumped anthropogenic food sources,[25] notably waste dumps, has been linked to artificially increased numbers of golden jackals (and resulting livestock predation problems) in the Golan Heights (Yom Tov *et al*., 1995) and in Bulgaria (Raichev *et al*., 2013). In the case of black-backed jackals, higher densities have been recorded near clumped resources such as carrion at seal colonies (Hiscocks & Perrin, 1988; Jenner *et al*., 2011; Nel, 2013) and at vulture restaurants (Yarnell *et al*., 2015).

Jenner *et al*. (2011) argued that in the Cape Cross Seal Reserve, clumped food resources (seal carcasses on the coast) were often shared by many jackals and that black-backed jackals in the reserve 'commuted' across the home ranges of others along well established paths, or 'jackal highways'. They argued on the basis of direct behavioural observations, that territoriality remained evident in that black-backed jackal pairs defended den sites (their core territories) through displays and vocalisations, and that intruders on the jackal highways avoided den sites and adopted suitably submissive postures when encountering resident pairs (Jenner *et al*., 2011: 235).

Black-backed jackal behaviour around clumped resources poses some challenges for how we understand territoriality. Hiscocks & Perrin (1988) argued that territoriality 'breaks down' in the presence of clumped resources, which in their study referred to large numbers of black-backed jackals feeding collectively on seal carcasses at the Cape Cross Seal Reserve in Namibia. A similar discourse of 'territorial breakdown' was adopted by Ferguson *et al*. to describe the tolerance of black-backed jackal pairs in the Kalahari for other

[24] Ferguson *et al*. found that home ranges tended to be smaller in the national park [where springhares (*Pedetes capensis*), hares (*lepus spp*) and mice were abundant (*ibid*: 498)]. In their assessment, this showed that the black-backed jackal can 'adapt to widely divergent ecological circumstances' (1983: 497). Home ranges may also change across seasons, once again pointing to the adaptability of this species (Humphries *et al*., 2016a).

[25] A study of coyotes in California revealed far higher densities of coyotes in landscapes where their prey base was supplemented by anthropogenic food sources (Fedriani *et al*., 2001).

jackals sharing water holes or ungulate carcasses (Ferguson *et al*., 1983: 496-7) and by Nel *et al*. (2013) with regard to black-backed jackals on the Namib Desert coast. More recently, du Plessis *et al*. (2015: 147) argued that a key question for future research into the management of black-backed jackals on farmlands was whether 'territorial breakdown' was occurring (presumably becoming more prevalent). We agree that more research on territoriality and home ranges is necessary, but caution that the term 'territorial breakdown' is confusing in so far as it might be read as suggesting a perfect overlap between home range and core territory and hence that when the home range is shared in some respects, 'territoriality' is somehow lost altogether. As McKenzie warns, home range use should not be equated with the true territory and that the 'essential feature with respect to home range use is the extreme flexibility and adaptability of the species' (1993: 368). The fact that black-backed jackals may allow the home ranges of their dispersing juveniles to overlap with the natal home range (Ferguson *et al*., 1983) also speaks to the flexibility of home range use.

The sharing of home ranges appears to be managed by social conventions suggestive of a wider understanding amongst black-backed jackals of hierarchies and the importance of signalling submission. Ferguson *et al*. observed that in the Kalahari Gemsbok national park, a pair of black-backed jackals with a home range around a watering point (a clumped resource) would allow other jackals (including other mated pairs) to drink – but that when they did so the latter showed submissive behaviour (lowered head, ears pulled back, tail drooping or tucked below the belly). The same pattern of submission to the resident pair was apparent at carcasses, where up to sixteen individuals were counted at one time (1983: 496-7). This suggests that black-backed jackals are able to access a set of social conventions (which as we noted earlier, are similar to pack behaviour) that recognise and reinforce hierarchies within the home ranges of dominant pairs whilst also facilitating access by other jackals to clumped resources.

2.3. Co-operative hunting and the 'cryptic pack'

Black-backed jackals are known to form hunting packs on an opportunistic basis (Moehlman 1987, McKenzie, 1990). For example, Krofel (2008) observed a black-backed jackal attacking a springbok trying to get out of a water hole in the Etosha national park (Namibia). The commotion attracted five other jackals who took part in the hunt. When it came to eating the springbok, the subordinate jackals were displaced from the carcass until the more dominant individuals had finished (*ibid*: 221). This is thus another example of how this normally solitary

hunter can access wider hierarchical and social conventions/behaviours when necessary to help co-ordinate collective efforts and to provide ordered access to resources.

McKenzie argues that the posturing and signalling conventions used by black-backed jackals are 'usually indicative of a complex social system common to canids that live in packs' (1993: 368-9). Based on 18 months of observations of black-backed jackals in Botswana, he concluded:

> 'The repertoire of social interactions in this species suggests a large social unit in which there is a need for ritualized control of potential conflict. I suggest that while jackals may live in pairs, the true social unit is a much larger 'cryptic' pack in which interaction and co-operation is facilitated by the well-developed social cues. In these 'cryptic' packs, the individuals are ready to co-operate when necessary, but function as apparently separate entities in the face of competition from the larger African carnivores' (1993: 369).[26]

The flexibility of black-backed jackal sociality and the tolerance of conspecifics within home ranges where there is abundant or clumped food resources poses challenges for those suggesting that small stock farmers should try to 'live' with their jackals rather than control their numbers through culling. The idea here is that farmers might be better off having a dominant territorial pair on their land, rather than killing them, thereby creating a 'sink' attracting (perhaps several) dispersing jackals. However, if a flock of sheep is like a clumped resource, or even just an abundant and easy food supply, then even dominant jackals on farms, like those on the Cape Cross Seal Reserve, might aggressively defend den sites, but tolerate other (suitably submissive) conspecifics in the area. Farmers are especially alert to the possibility that a dominant jackal pair might share their home range with others. Consider the following comment (from 2009) by member of a South African hunting website:

> 'The story that the good jackals keep others away is not entirely the truth. I sat on a particular farm, about four years ago and within two

[26] McKenzie, a veterinary scientist, drew direct implications for the management of rabies, arguing that aggression (and biting) between black-backed jackals is likely to be higher (and the risk of spreading rabies greater) in areas where they are persecuted because the remaining and newly arriving jackals are likely to be setting up a new social order, and hence struggles over hierarchy could lead to higher incidents of fighting. He thus recommended against killing black-backed jackals (and hence disrupting their regional social system) as a rabies prevention strategy, but rather to concentrate on vaccinating domestic dogs against the disease.

> hours I had shot 11 adults, without moving from my spot. It was June and there were five pairs and a really old male whose mate had almost certainly died of old age. How come the dominant jackal pair had not done their work???' (translated from Afrikaans).[27]

This comment reflects a broader scepticism within the South African sheep farming community about non-lethal approaches to black-backed jackals, especially the hypothesis that allowing a dominant pair to live on the land will keep other jackals away (see Nattrass & Conradie, 2015). While this is a possible outcome, it ignores the available evidence regarding the black-backed jackal's flexible social arrangements, including tolerance for conspecifics depending on the context. There may, in other words, be no simple or general solutions to mitigating conflict with the black-backed jackal by assuming that jackals are distributed across the farming landscape in discrete territories with minimal overlap.

3. Black-backed jackals as 'problem' animals for farmers and wildlife managers

Black-backed jackals can be a problem for both farmers and managers of national parks. They may kill sympatric endangered felines like *Felis nigripes*, the black footed cat (Kamler *et al*., 2015) and in closed reserves, which limit dispersal and are often only proxies of natural ecosystems, black-backed jackals can potentially threaten the viability of select ungulate species particularly those that rely on hiding their fawns as an anti-predator strategy (Klare *et al*., 2010).[28] Kaunda observed pairs of black-backed jackals in a nature reserve hunting for impala lambs, noting how they would inspect the herds for signs of recent birthing and then one would distract the mother while the other would kill the lamb (1998: 81). They would also attack mothers in the process of giving birth, killing the new born and injuring the mother also, sometimes fatally (*ibid*: 81-82). On farmlands black-backed jackals appear to target the lambs, rather than adult sheep and have been known to attack cows in the process of calving, feeding on the calf as it emerges, and on the cow's udder and inside flanks

[27] Available on http://jaracal.com/viewtopic.php?f=21&t=3&start=100 (accessed 12 December 2016).

[28] The fawns of hider species of ungulates have been found in the scat of black-backed jackals in two conservation areas in the Eastern Cape (Brassine, 2011). This concurred with an earlier study of black-backed jackal stomachs removed from animals culled on farms and in a reserve where hoof remains indicated that newly born and young antelope were frequently preyed upon (Grafton, 1965: 44).

(Skead, 1979: 28; PMF, 2016: 35). There is some evidence, however, that where wild fawns are available on farmland, jackals prefer them to domestic animals (Kamler *et al*., 2012b).[29]

As discussed earlier, black-backed jackals are opportunistic feeders making it difficult to pin-point their ecological impact (which will vary according to context) or the extent to which they pose a threat (directly and on balance) to small stock farmers. Whether they hunt or scavenge is an important issue, as is the extent to which black-backed jackals living in protected areas pose a threat for neighbouring sheep farmers. Kaunda reported black-backed jackals bringing carrion and pieces of sheep they had killed on farmlands back into the reserve (1998: 82). A later study of stomach contents of black-backed jackals killed in the Transvaal in hunting and culling operations on farms and in the reserves during the late 1960s found that carrion, rodents, hoofed domestic stock (mostly sheep) insects and hares (*Lepus capensis*) were the major sources of food by volume and frequency of occurrence (Bothma, 1971b). Twenty seven percent of the stomachs from farmlands contained domestic stock, and 6 percent of stomachs from the game areas contained domestic stock (*ibid:* 199).[30]

A study of black-backed jackals killed by vermin clubs in the Transvaal, mountainous parts of Natal, the Free State and the Western Cape of animals on farms and in nature reserves with access to farms found that carrion (identified by maggots and putrefied flesh) formed the bulk of the diet (Grafton, 1965).[31] In the reserves, the carrion was mostly antelope, on farms it was mostly sheep (*ibid*: 44). Reflecting on these findings, Grafton observed:

> 'There is no way of determining whether fresh sheep remains in a stomach are of a sheep killed by the jackal or from one which died of some other cause and was subsequently fed upon by the jackal. In either case, the stomach is recorded as having contained sheep remains

[29] This is consistent with evidence from coyote predation of lambs in Idaho. A six year study of coyote density and predation on sheep found that increased losses of lambs resulted from reduced buffering of natural prey (notably declines in lagomorph densities) (Stoddard *et al*., 2001).

[30] Bothma concluded that further research should concentrate on changes in diet over seasons and on the prey items consumed in relation to prey availability, and that further analysis of the stomachs of these opportunistic feeders would not add much to our knowledge about black-backed jackals (1971b: 202).

[31] The black-backed jackal stomachs also contained rodents, small carnivores (mongoose, dog, cat), antelope (mostly fawns), insectivores (hedgehog, shrews), hoofed domestic stock, reptiles, birds, insects, myriapods (centipedes etc.), crustaceans, arachnids (mostly spiders, sometimes scorpions), vegetable food (ground nuts, grapes, berries, fruit) and items such as bark, grass, grit, newspaper (Grafton, 1965).

> as a result of jackal depredation. The converse occurs however when rotten sheep remains are found in a stomach. This material is recorded as being carrion regardless of whether the sheep might possibly have been killed by the jackal and was then fed upon over a period of days by which time the remains would be rotten and maggot-infested. The errors just described will balance each other to some extent. The writer believes, however that the error of carrion being recorded as sheep [killed by jackals] is more frequent than the converse and that many sheep mortalities ascribed to jackal depredation are in fact the result of other causes. This is particularly so in marginal sheep areas where the condition of stock is poor and the care bestowed upon the flocks is generally of a low order' (Grafton, 1965: 51).

It is possible that black-backed jackals target sicker or weaker prey because it is easier to catch. A study of predation of small stock in a communal farming area in Namaqualand (in the Northern Cape) found that animals in poor condition (usually a function of drought) were more likely to be lost to predators than those in better condition (Lutchminarayan, 2014: 18-19). When kraaling was common on commercial sheep farms (before the advent of industrial jackal-proof fencing and artificial water sources), farmers noted that predation by jackals was worse during drought years (Beinart, 2003: 214) when animals were weaker (and presumably also there were fewer wild prey).

A more recent study of black-backed jackal scat on farmlands in the Karkloof (KwaZulu-Natal, South Africa) found that over half of the biomass consumed was rodents, but that about a quarter comprised domestic livestock, mostly cattle (Humphries *et al*., 2016b). Given that this was a scat analysis, the researchers could not distinguish between carrion and fresh kills. The researchers had observed black-backed jackals hunting sick cattle and attacking newborn calves (*ibid*: 5) but noted that farmers also left dead livestock out in the open. Interviews with 57 farmers in the area revealed that less than half buried dead livestock, and that the rest did nothing or relied on vultures to dispose of dead animals (Humphries *et al*., 2015).

Black-backed jackals have been observed caching carrion on the Namibian coast (Hiscocks & Perrin, 1987: 57) and Kaunda, in his observational study of black-backed jackals in Botswana, recorded:

> 'Black-backed jackals were also observed caching freshly caught prey on five occasions, and retrieving caches on two occasions. Two rodents were cached whole, whereas only remains of one impala lamb, one scrub hare and a chunk of ungulate carrion were cached. Prey was

> cached some distance away from the kill. Caching involved digging a shallow hole in a concealed place, usually under some shrubs, and covering the food with soil and/or vegetation. All caches that were observed took place after a jackal had eaten at a kill, usually within 10 min' (1998: 83).

Drawing on insights from hunters and farmers, the South African Predation Management Forum (PMF) states categorically that black-backed jackals 'will not move the carcass from the killing site' (2016: 36). However it is possible that cached carcasses are being overlooked. Farmers often complain that their lambs can 'disappear without trace', making it impossible for them to identify the cause of death (personal communications from many farmers and farmer meetings). Caching may be one reason for this, especially given that coyotes are known to cache food and that this has been postulated as one of the reasons for why sheep farmers sometimes cannot account for missing lambs (Knowlton *et al*., 1999: 404). In Namibia, black-backed jackals have been known to move their freshly killed prey to more sheltered areas before consuming it (Goldenberg *et al*., 2008), so moving prey from a kill site might also be occurring. However, black-backed jackals are probably also being blamed for loss of sheep and lambs due to theft by humans.

A study by the Natal Parks Board in the early 1970s on the impact of jackal predation on five farms in Natal (near the Kamberg Nature Reserve and approximately the area of the Kamberg Vermin Hunt Club) confirmed 332 kills attributed to black-backed jackals, amounting to 0.05 percent of the sheep population. Most sheep predations occurred in the winter and spring when there was an abundance of lambs (Rowe-Rowe, 1975: 80). However, the study also found more than twice as many sheep were lost to other causes such as diseases or accidents (*ibid*: 81). The study observed that outlay on fencing materials for temporary enclosures would probably pay dividends, noting that 'while much was spent on drugs and disease prophylactics nothing was spent on protection against jackals' (*loc.cit*).

This confirmed the results of an earlier study (Grafton, 1965) of black-backed jackal stomachs from animals killed by hunt clubs in South Africa (mostly in the Transvaal). The sample was biased towards sheep-killing jackals because dead jackals were collected from professional hunters who had been called to areas with perceived predation problems (*ibid*: 45). Even so, the bulk of the food was found to be carrion, suggesting that 'many sheep mortalities ascribed to jackal depredations are in fact the result of other causes' (*ibid*: 51). The study also emphasised the 'omnivorous habits of the black-backed jackal which includes

many so-called pest species (e.g. rodents) in its diet, even in sheep farming areas' (*ibid*: 52):

> 'Volumetrically, domestic stock, poultry and birds amount to 24 percent of the food taken while rodents, hares and insects total 27 percent. Foods of no apparent interest to the farmer make up the remainder of the diet. The conclusion may be drawn that the black-backed jackal's food habits are in many ways beneficial to both crop and sheep farmers and that the animal exerts considerable ecological influence upon the fauna of its environment. Jackal control measures should therefore be applied with caution and should be selective towards only those individuals known to be predators on domestic stock' (Grafton, 1965: 52).

The idea that some individual black-backed jackals may be more likely to predate on sheep than others, and hence that the 'problem animal' rather than the species should be targeted, has a long history. As discussed in Nattrass *et al*. (2017), Douglas Hey, the Director of the Western Cape Department of Nature Conservation, argued that there were 'criminal' individual predators, just like there are criminal humans and hence one should not persecute the entire species. He supported the coyote getter (which could be placed near lambing pens) and hunting with hound packs (because dogs can pick up the trail of a black-backed jackal at a freshly killed sheep) precisely because they were more selective methods than simply killing predators.

Studies have shown that not all coyotes are sheep killers, and that sheep killers were typically territorial breeders (see review in Knowlton *et al*., 1999: 403). A study from Northern California demonstrated for coyotes that sheep depredation can be caused by relatively few individuals. Sacks *et al*. found that two breeding males were responsible for almost all of the kills on a sheep farm that they were monitoring and that when these individuals were removed, sheep depredation declined precipitously – and that the removal of other coyotes had no effect (1999: 598-9, 601). They conclude that 'the residency of a pair that did not kill sheep in an area where sheep were pastured would be expected to reduce depredation if the pair's presence kept other coyotes from killing sheep in their territory' (*ibid*: 602). Conversely, they warn that 'removal of breeders from territories overlapping sheep, but where predation is not a problem, may be counterproductive by allowing access to sheep by potential sheep-killing coyotes' (*ibid*: 603).

This supports the 'live with the jackal' recommendation. However, whether the coyote literature applies to black-backed jackals remains to be determined,

although there are some indications that particular individuals target sheep more than others. A stock farmer near Graaf Reinet observed a female black-backed jackal over three years and determined that she did not eat his sheep. However, her mate did, and each year he shot the mate, hoping that she would eventually find a mate who shared her preference for wild prey (personal communication). He also had a caracal mother and kittens on his land, and refused to allow his workers to kill them (saying they were 'too beautiful'). This particular farmer suffered from persistent theft and eventually gave up farming sheep altogether in favour and concentrated on cattle. He reported no predation of calves.

Another difficulty with the 'live with the jackal' strategy is that there is no guarantee that offspring of a non-sheep eating pair will share their preferences (though they might) and dietary preferences might change, especially if the supply of wild prey declines. Given how productive black-backed jackals are, it is possible for their numbers to expand quickly, potentially causing significant local declines in prey populations, thereby posing a potentially growing problem for small stock farmers. A farmer from the Eastern Cape reported that he used to hunt black-backed jackals because of their depredation on his sheep, but that after he stopped farming sheep (because of the depredation), the small game on his land was totally decimated,[32] and he presumed this was a result of predation by black-backed jackals. He asked the PMF for advice and was advised to contact a professional jackal hunter.[33]

When thought to be responsible for precipitous declines in populations of springbok and other ungulates, black-backed jackals have been actively culled by conservation officials in South Africa. They were hunted by the Natal Parks Board between 1953 and 1971 (Rowe-Rowe, 1975: 79) and in the late 2000s and early 2010s SANParks culled jackals in several Karoo national parks. Unpublished observations by conservation officials suggest that culling black-backed jackals in 2009 in the Addo Elephant National Park (in the Darlington Dam area) just before the springbok lambing season helped the springbok population to recover but that it probably also allowed the ostrich population to grow rather too large (personal communication). In any event, black-backed jackal numbers were generally perceived to have bounced back within three years in national parks where they have been culled.

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[32] His observed decline in the wild prey base could have resulted from other causes, such as drought, over-grazing, disease etc. – or it could be the case that the presence of black-backed jackals altered their behaviour, perhaps making them more difficult to observe (for the broader impact of predators on the prey base, see Pekarski *et al*., 2008).

[33] See: http://www.pmfsa.co.za/home/ask-our-expert/item/217-protection-of-game-against-jackal (accessed 10 December 2016).

The capacity of black-backed jackal numbers to rebound after persecution is well known. As Bingham and Purchase observe, their average productivity rate (viable offspring produced per adult jackal per year) of 1.5 means that black-backed jackal populations are 'capable of rapid recovery following population crashes' and that 'only very intense culling would have any significant effect on jackal populations' (1983: 25, 1999). The same is true for red foxes in France (Lieury *et al*., 2015), and indeed for most mesopredators. As Prugh *et al*. put it, lethal control 'can thus be likened to moving a lawn, in that persecution induces vigorous growth in the mesopredators population' (2009: 784f; see also Knowlton *et al*., 1999).

While there are observational studies and analyses of scat and stomach contents which support the assumption that black-backed jackals can pose a threat to springbok populations, drawing a direct line between the fact that they eat springbok fawns and declining ungulate numbers is fraught with uncertainty. Notably, it is difficult to tell whether mortality due to black-backed jackals is compensatory (the animal would have died of other causes, such as starvation) or additive (the animal would have lived if not for predation by the black-backed jackal). For example, coyotes were blamed for the decline in kit foxes (*Vulpes macrotis*), a protected species, on a reserve in California, so coyotes were killed between 1985 and 1990, but with no measurable impact on the kit fox population (Cypher & Scrivner, 1992). Cypher & Scrivner note that the decline in kit foxes was associated with the decline in lagomorphs (black tailed jack rabbits (*Lepus californicus*) and desert cottontails (*Sylvilagus audubonii*) and hence argue that coyote predation was probably compensatory (*ibid*: 45).

Black-backed jackals have been known to consume at least seventeen different carnivore species (Bagniewska & Kamler, 2013: 566). These include the African wild cat (*Felis silvestris lybica*) (Bothma, 1971b), aardwolf (*Proteles cristata*) (Brassine & Parker, 2012), bat-eared fox (*Otocyon megalotis*) (Klare *et al*., 2010), caracal (citations in Bagniewska & Kamler, 2013: 566), domestic cat and dog (Grafton, 1965), genet (*Genetta genetta*) (Klare *et al*., 2010), yellow mongoose (*Cynictis penicillata*) and striped polecat (*Ictonyx striatus*) (Kamler *et al*., 2012b). Manipulation of their numbers may thus impact food webs in unknown ways and cause trophic cascade lower down the food chain.

Culling black-backed jackals on farmlands could also have adverse trophic consequences for farmers. For example, black-backed jackals are known to suppress hare numbers (Bagniewska & Kamler, 2013), so killing then could increase hares and hence place additional pressure on grazing. Some farmers appreciate the role that black-backed jackals can play in controlling hares and rodents, even to the point of desiring them back on their land. For example, a

farmer from KwaZulu-Natal posed a comment on an internet conversation string about the problems posed by black-backed jackals asking where he could 'buy' some jackals. When others responded in amazement, telling him that he should 'just buy a sheep, the jackals will come!'.

He responded:

> 'I HAVE some sheep but no jackals. Perhaps not endemic so close to the coast?? Believe it or not I want to use THEM for pest control. I have done it before and provided you keep the jackal population small, while they have easy prey they will even leave sheep alone, but once they have sorted out the other pests, beware'.[34]

However, there are other predators of hares and rodents, notably caracals and foxes, so it is not always the case that removing black-backed jackals from a farm will result in a rise in such 'pest' fauna because other predators might fill the niche. We have been told on two occasions that farmers have found caracal kittens in the stomach of a black-backed jackals they have killed, suggesting that there might be a complex ecological relationship between these two species (see also Hey, 1967: 160). Also, if black-backed jackals had been controlling stray dogs, then killing black-backed jackals could result in an increase in sheep predation by domestic dogs. Black-backed jackals are known to suppress Cape Fox (*Vulpes chama*) populations (Kamler *et al*., 2013) hence removing black-backed jackals is likely to increase Cape fox numbers and that this too will affect the ecology of the area.

As Du Plessis *et al*. (2015) note, information about the ecology of black-backed jackals on farmlands is limited. They argue that more scientifically grounded studies are necessary. We concur with the need for more research but are less optimistic about the potential of such research to provide anything approximating a 'full picture' given the diversity of physical and climatic conditions, varying land-use types, different management strategies on farmlands, stocking densities etc. – all of which are likely to affect black-backed jackal diet and behaviour. Even if it were possible to conduct scientific studies with appropriate randomised controlled experimental designs in all these differing contexts, the wild card is always the ability of black-backed jackals to adapt and disperse over long distances, thus potentially disrupting existing ecologies. An even bigger disruptive influence on local ecologies is of course humankind both at the local level and at the global via climate change. Studying the black-backed jackal is thus always likely to be a moving target.

[34] See http://www.encounter.co.za/article/177.html#Comments

3.1. Prevention versus lethal control

Given the likelihood that lethal control of black-backed jackals will provide only a temporary solution (and could even make things worse depending on the particular ecological circumstances) for farmers, increasing attention is being paid to non-lethal methods of protecting livestock (PMF, 2016). In particular livestock-guarding dogs have been trialled in Namibia, and according to surveys of participating farmers, they are perceived to have helped reduce depredation significantly. It should however be noted that two-thirds of the dogs worked together with herders (Marker *et al*., 2005). In South Africa, McManus *et al*. (2014) conducted a before and after quasi-experiment[35] on 11 participating farms in the Eastern Cape where in the first year, farmers practiced lethal control, then in the next two years said they used only non-lethal methods. Three farms received livestock guarding dogs, one received alpacas and the other seven received 'dead stop' (steel) livestock protection collars (2014: 3). In the year of lethal control, farmers lost on average 14.3 percent of their stock. In the second year (i.e. the first year of non-lethal control) they lost an average of 4.4 percent of their stock, and in the third year 3.7 percent of their stock (*ibid*: 4). All farms experienced lower cost in the years of non-lethal control (*ibid*: 5). However, a follow-up after 13 months revealed that only 6 of the 11 farms continued to use non-lethal control (mostly those with guardian dogs) and the other five used a mixture of lethal and non-lethal methods. A follow up 30 months after the end of the trial revealed that only four of the original farms continued to use only non-lethal methods, five used a mixture of lethal and non-lethal and two had switched back to lethal control only (*loc.cit*). The authors conclude that non-lethal methods were cost-effective, but fail to comment on why farmers steadily switched back to including lethal-control in their management toolbox.

Treves *et al*. (2016) reviewed existing studies from the US and Europe of lethal and non-lethal control of carnivores and found that only 12, in their assessment, met the accepted standard of scientific inference (random assignment or quasi-experimental case-control). Of these only six demonstrated predation prevention (four non-lethal and two lethal interventions), two lethal interventions showed an increase in predation and the remaining four (one non-lethal and three lethal) showed no effects. They conclude that policy makers should suspend predator control efforts that lack evidence for functional effectiveness and that more and

[35] The study lacked a control site (i.e. farms where lethal control took place over all three years), and the authors did not discuss the possibility depredation in the second year might have been depressed by lethal control in the first year. Despite these limitations, McManus and others classified this study as a 'pseudo control, case control design' (Treves *et al*, 2016: 385) which in our view is overly generous given what the study actually entailed.

better designed scientific studies are needed. We concur with the need for better designed studies, especially in systems that lack research (i.e. farmlands) but caution against the assumption that this will allow us to draw strong generalisations about the effectiveness of a particular method – as these are likely to vary across space and time as black-backed jackals adapt to persecution and as humans continue to transform the environment.

It is also important to note that the distinction between lethal and non-lethal methods is a grey area, especially where livestock-guarding dogs are concerned. An interview-based study of 73 farmers in Namibia who had adopted Anatolian live-stock guarding dogs (83 in total) provided by a non-governmental organisation (Cheetah Outreach) found that all farmers said they had stopped killing leopards and cheetah, though one reported that the dog had killed a cheetah (Potgieter *et al*., 2015). However, more black-backed jackals were killed by farmers and dogs than was the case before dogs were introduced and two of the dogs killed non-target carnivores (a bat eared fox and an 'unknown' number of African wildcats) and 15 killed prey species [notably Eland (*Taurotragus oryx*) and Oryx (*Oryx gazella*) calves]. The authors conclude that 'livestock guarding dogs in Namibia cannot be considered a non-lethal means of predator control, particular with respect to medium sized carnivores' (*ibid*: 7).

Fencing can also result in the death of animals through entanglement in fence wires, or by preventing migratory species from moving across the landscape. Electric fences in particular have also been found to have lethal consequences for many animals, especially porcupines, tortoises and snakes (Burger & Branch, 1994; Beck, 2010), the general recommendation being that low-level trip wires should be discontinued in favour of rock-packed aprons and that fences be switched off during the day.

4. Rapid adaptation and implications for management

The success of the black-backed jackal in human modified environments may be attributed to their opportunistic and generalist diet, flexible social structure, and an ability to learn from experience and adjust their behaviour rapidly. According to Brown & Wilson (1957), closely related carnivore species are more likely to show 'character displacement', differing in their behaviour, morphology and ecological niche in the zone of sympatry (where they overlap geographically) than where they are allopatric or in non-overlapping regions. This suggests that adaptation and evolved differences occurs relatively quickly and in

geographically distinct ways amongst carnivores. The black-backed jackal is likely to be no different in this regard.

The capacity of black-backed jackals to adapt is evident also in their hunting strategies. In the Addo Elephant National Park they have perfected a technique of breaking ostrich eggs using one as an anvil (Hall-Martin & Botha, 1980 – see also Fitzsimons, 1919: 103). They have been seen robbing gulls of the shell fish they harvest and then drop on rocks in order to crack them open (Hiscocks & Perrin: 1987: 57). Kaunda reports in a nature reserve in Botswana:

> 'Jackals were also sensitive and responded to the flight patterns of vultures, eagles and raptors. If a jackal observed avian predators or scavengers making a rapid descent and landing, it would swiftly run to the spot to investigate any potential food source' (1998: 58).

Observations from the Namib Desert suggest that jackal gait varies depending on topography, which suggests a 'dynamic adaptation to a demanding environment' (Goldenberg *et al*., 2008). In the wind-swept Namib Desert they take their food to sheltered areas (resulting in the formation of middens) and this appears to be the only place they do this (Avery & Avery, 1987). Deacon (2010) argues, on the basis of GIS data collected by hunters of black-backed jackals killed in the Southern Free State between 1993 and 2009, and his own identification of black-backed jackal dens in 2008 and 2009, that den sites on small hills facing east with relatively thick vegetation were favoured year after year. He argues that this strong relationship between physical characteristics of the land and optimal black-backed jackal den sites can be exploited by farmers in their efforts to find and destroy them. However, black-backed jackals are also known for their rapid learning/adaptation to persecution by humans. Most notably, they are nocturnal on farmlands where they are persecuted, and diurnal in reserves (Mckenzie, 1993: 368).[36] As Fitzsimons observed nearly a century ago, black backed jackals are 'frequently seen abroad during the daytime' in the 'wilder districts …far removed from the European colonist… but it has long since learned to dread the white man with his gun and consequently takes the greatest of precautions to conceal itself when he is about' (1919: 92-3). A study of golden jackals in Ethiopia found similar patterns, notably that 'foraging activity was confined to the night and the jackals tended to rest during the day in habitats providing cover from human disturbance' (Admasu *et al*., 2004:151).

[36] Black backed jackals are diurnal in the Cape Cross Seal Reserve in Namibia (Hiscocks & Perrins, 1988: 99).

4.1. Adapting to persecution

Black-backed jackals, like coyotes, adapt to persecution. When the existing pattern of territories and social hierarchies is disrupted through hunting/culling, there is less competition for food and breeding vacancies emerge. This allows females to start breeding at a younger age, have larger litter sizes and higher pup survival rates. A study of the impact of removals on coyote populations found that populations soon rebounded (within eight months) to pre-removal levels (Gese, 2005). Gese argued that the density of coyotes in any particular area is 'dictated by food abundance as mediated by social tolerance' (Gese, 2005: 281).

Black-backed jackals are also known to adapt quickly, and at an individual behavioural level to traps, other hunting techniques and livestock protection devices. There are no scientific studies in South Africa on the adaptability of black-backed jackals to trapping and hunting on farmlands, though there is considerable local knowledge on the subject, especially from jackal hunters. Niel Viljoen (2014), the South African Red Meat Industry predator specialist, argues that young, inexperienced black-backed jackals may be responsive to prevention devices (noises, lights) at least for a few months and that call and shoot methods work well at this age but that all methods are less effective regarding older, more experienced jackals. Other professional jackal hunters complain that it has become harder over time to succeed at night shooting because the black-backed jackals have grown 'wary' of the lights (personal communications). Researchers complain that jackals are very difficult to catch, even to the point of suspecting that a jackal who manages to escape a soft-trap somehow communicates this to the rest of the jackals in the area (Pinnock, 2012). A black backed jackal has been filmed approaching a gin trap on its stomach and tapping it from a horizontal position in order to spring it without any harm coming to the jackal (*ibid*).

A study of coyotes on a northern California sheep ranch involving capture and recapture of radio-collared coyotes found that they were much harder to trap than in other areas, suggesting that the population in this area had adapted to regular control measures (Sacks *et al*., 1979). Juvenile coyotes were easier to catch, though still difficult suggesting that they had 'learned avoidance of devices or general 'wariness' from their parents or other coyotes' (*ibid*: 944). They also struggled to catch the mates of radio-collared coyotes, even though they were likely to be in the vicinity of the radio collared animal.[37] They 'set

[37] NB: Marine Drouilly never managed to catch any of her radio-collared jackals' mates, despite trying hard and most of her trapping success on farms was of sub-adult black-backed jackals.

many traps where these individuals left sign, only to have them ignored, dug up, or defecated upon' (1999: 945). The authors argued that trapping success was biased towards the younger, non-breeding coyotes who were the least likely to depredate on sheep.[38] They thus observe that 'more conservative use of devices might increase their effectiveness by reducing the potential for resident breeders to learn avoidance of devices' (1979: 947). Black-backed jackal hunters in South Africa make a similar point, often blaming the unprofessional use of the FoxPro (a set of taped wildlife 'calls' that can be played at night to attract jackals) for 'training' black-backed jackals in how to avoid them (see Nattrass *et al*., 2017).

Back in the 1960s, Douglas Hey observed that the coyote-getter was reasonably effective, but that faults in the design allowed some to get away and that 'one seldom has a second chance at a smart jackal' (1967: 159). Bothma (1971a) examined data on black-backed jackals killed by coyote getters in the Transvaal in the 1960s, finding that almost all kills were soon after the getter was set, and that kills became negligible after two weeks. He thus recommended that getter control efforts never exceed two weeks in any area (*ibid*: 187).

An experimental study of black-backed jackals on the South African Northern Cape coast, in a non-farming area, showed how quickly black-backed jackals learned to avoid coyote getters (Brand *et al*., 1994). Between 1985 and 1988 the kill rate declined and the avoidance rate increased, with adult females being the least likely to be killed. Brand *et al*. note that this could be 'attributed to jackals 'pulling' coyote getters but escaping death (i.e. individual learning) or jackals directly observing a conspecific (e.g. mate or parent) actively avoiding the device (i.e. social influence) or observing another individual being killed (i.e. social learning)' and that similar ''increased shyness' to coyote getters had been observed in dingoes and kit foxes' (1994: 46). Brand *et al*. argue that the difficulty in killing adult females could be because they might have experienced the death of their pups from coyote getters and may even teach fear of coyote getters to subsequent litters (*ibid*: 46-7). They observe that this could also explain the bias in sex ratio of jackals killed (towards male back-backed jackals) in other studies (*ibid*: 47). Bothma (1971a) also found a sex ratio skewed towards males in his study of black-backed jackals killed by coyote getters in the Transvaal in the 1960s.

Brand & Nel (1996) followed up their study with experiments conducted on captive black-backed jackals exposed to bait and cyanide guns (firing a bitter tasting but non-lethal capsule). They found that the black-backed jackals were more suspicious of bait plus the gun than they were of bait alone and that the

partners of black-backed jackals who were shot by the bitter capsules learned to avoid the guns. They concluded that the inherent and acquired behavioural patterns of black-backed jackals was likely to lead to the less effective use of cyanide guns in areas where control operations are conducted (Brand & Nel, 1976: 181). They note that their results are compatible with observations from those engaged in hunting operations (cited in *ibid*: 177) that black-backed jackals become more wary over time. Kaunda (2001) found that black-backed jackals in Mokolodi Nature Reserve in Botswana were very hard to capture with a variety of baits, especially commercial baits or livestock baits. He concluded that his study suggested evidence of neophobia (aversion to novel stimuli) and that black-backed jackals may have also come to fear the kinds of baited traps found on farmlands (*ibid*: 45-6). Professional black-backed jackal hunters concur. Niel Viljoen, who has observed jackals on his farm for many years, tells the story of how just placing a small stone on the lip of a water trough resulted in the jackals avoiding the trough for five days. This story has been repeated to us many times by farmers in the Karoo as an illustration of how sensitive black-backed jackals are to any human-induced changes to their environment.

It is common knowledge amongst contemporary South African sheep farmers that prevention technologies such as noise deterrents work for a few weeks or months at best, and that it is important to keep black-backed jackals out of stock pens, especially during the lambing season, and to use guard animals and herders where possible (Verdoorn, 2016). Black-backed jackals adapt quickly to devices like bells on collars, so farmers are advised to use more than one method and to alternate them regularly (Landman, 2016; PMF, 2016).

The adaptability of black-backed jackals to local conditions makes them very challenging to study. For example, a study of black-backed jackals killed by culling operations in national parks in the Karoo and the Eastern Cape and on surrounding farmlands (Minnie *et al*., 2016) found that culled black-backed jackals were younger on the farms. This coupled with the fact that these younger jackals had a lower age of first pregnancy and larger litter sizes, led the authors to conclude that it was consistent with 'source-sink' dynamics (dispersal into farmlands). Such dynamics are likely and are evident also for coyotes (Knowlton *et al*., 1999; Gese, 2005). Yet the differing age structure of culled black-backed jackals probably also reflected the fact that older black-backed jackals with experience of hunting, are more difficult to kill than juveniles (Brand *et al*., 1995), thereby potentially confounding the study.[39]

[39] Minnie *et al*. argued that the culling was done the same way in both study sites (call and shooting of all jackals responding to calls) and that this reduced 'potential biases in sample collection' (2016: 382). However, if older jackals on farms have become wary of call and shoot operations (as claimed by many farmers and hunters we have spoken to), then older

Although black-backed jackals are very difficult to eradicate on farmlands, it is important to recognise that they have been controlled in the past, in many sheep-farming areas. As discussed in Nattrass *et al* (2017), government subsidised fencing and predator control, together with collective action to 'clean' jackals out of enclosed farmlands, resulted in the effective exclusion of jackals for many decades from sheep farms in the Karoo. Contemporary discourse about the impossibility of excluding this wily predator implicitly assume that such level of support for predator control and exclusion is unlikely to occur now or in the future.

4.2. Implications for management

In short: the black-backed jackal is a highly flexible predator whose behaviour and diet adapts to the environment and to persecution. We highlight the following conclusions from our review of the literature for how to think about managing the dynamic human-wildlife conflict between farmers and black-backed jackals:

1) Compared to other African jackal species, the black-backed jackal outside of nature reserves avoids human settlements and has teeth appropriate for both omnivory and eating meat. It is a coursing predator that is also adept at finding and eating lambs and fawns of ungulates that hide their young (including of domestic livestock) and at scavenging carcasses on farmlands and in reserves. The availability of wild prey and of carcasses on farmlands can provide alternative food sources, thereby potentially reducing the risk of predation on livestock, but it may also increase black-backed jackal densities (thereby ultimately increasing the risk of depredation).

2) Black-backed jackals draw on a wide range of food sources, and some individuals may have less of a 'preference' for domestic stock than others. Where there is a wild prey base on a farm, killing the dominant jackal pair might be counter-productive if the territory is opened up to dispersing individuals with a greater preference for lambs.

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black-backed jackals are less likely to be shot on the farms than juveniles. Furthermore, given that there was a cull in two of the national parks in 2010, it is possible that juveniles in those parks were disproportionately harvested then, leaving an older population in the parks, further biasing the samples.

3) Black-backed jackals operate within a loose, flexible social structure with clear social signals and hierarchies. Individuals can 'commute' across the home ranges of conspecifics (assuming a subordinate demeanour), thereby making it possible for black-backed jackals to obtain food sources from outside their core breeding territories.

4) Black-backed jackals are productive breeders. The natural regulation of black-backed jackal numbers occurs through the effect of food availability on litter size (and age of breeding females) and through social mediation (females with territories are more likely to breed and non-breeding juveniles will disperse to find new territories). Hunting and culling black-backed jackals on farms will thus result in vacant territories potentially to be colonised by dispersing individuals. Culling and hunting, unless done both intensively for prolonged periods and extensively across a large landscape and accompanied by measures to exclude the entry of dispersing jackals, is thus likely to have a limited impact beyond the short-term.

5) Black-backed jackals adapt to lethal control such as traps, coyote getters and night-hunting through individual and social learning. They also adapt quickly to different deterrents, hence protective devises and deterrent strategies need to be rotated, mixed etc.

6) Non-lethal approaches are important. However, the distinction between lethal and non-lethal methods is not as clear cut as commonly supposed: livestock guarding dogs kill predators and other animals; fences cause deaths through entanglement and electric fences especially kill snakes and reptiles.

The central finding from a management perspective is thus that there is unlikely ever to be a unique or simple solution to human-wildlife conflict involving black-backed jackals and livestock farmers. Black-backed jackal behaviour is likely to vary across space and individuals, be affected by the presence of competitors, local ecologies, human persecution, and by the availability of food. The unstable mix of lethal and non-lethal responses that appears to have emerged on South African small stock farms is likely to continue.

Hopefully further research can help shed light on what is in all probability South Africa's most vexing conservation conflict. Local knowledge is important hence there is a crucial role for inter-disciplinary research that includes diverse stakeholders, including farmers, and seeks to influence policy and management through collaborative, open and trustful engagement.

Appendix 1: Selected Annotated Literature on black-backed jackals in Southern Africa

Citation	Area of study	Key findings
Avery, G., Avery, D.M., Braine, S. & R. Loutit. 1987. Prey of coastal black-backed jackal *Canis mesomelas* (Mammalia: Canidae) in the Skeleton Coast Park, Namibia. *Journal of Zoology*, 213(1): 81-94.	Skeleton Coast Park, Namibia. Looked at jackal middens (accumulate on tufts that provide shelter)	Study found that black-backed jackals were unselective in their scavenging of dead birds, fish, penguins etc. and that middens could be a useful index of changing fish stocks, climate change (e.g. effect on declining penguin numbers).
Bagniewska, J.M. & J.F. Kamler. 2014. Do black-backed jackals affect numbers of smaller carnivores and prey? *African Journal of Ecology*, 52(4): 564-567.	Study of black-backed jackals in a private game farm, private stock farm and a nature reserve. Near Kimberly. Used scent stations to get presence and transects to look at all species	The found a negative relationship between black-backed jackal presence and the numbers of hares (*Lepus capensis and L. saxatilis*), yellow mongoose (*Cynictis penicillata*) and ground squirrel (*Xerus inauris*). This is unsurprising given that Klare *et al*. (2010) found that in the game farm (they both studied the same game farm) ground squirrels had a 19-36% frequency of occurence in jackal diets, and hares (2-27%) and yellow mongoose (0-12%), cited on page 56. Study site was Rooipoort Nature Reserve, Benfontein Game Farm and private farms.
Bernard, R.T.F. & C.T. Stuart. 1992. Correlates of diet and reproduction in the black-backed jackal. *South African Journal of Science*, 88(5): 292-294.	Black-backed jackals in the Western Cape. Unclear where – they used killed jackals, so probably most if not all on farmlands.	Found that black-backed jackals reproduce in the winter – unlike other small canids such as side-striped jackals, bat-eared foxes and Cape foxes which reproduce in the spring and into the summer. The authors speculate that this is due to diet, with the black-backed jackal specialising on scavenging ungulate carcasses on the veld.
Bingham, J. & G.K. Purchase. 2002. Reproduction in the jackals *Canis adustus* Sundevall,	Study of black-backed and side-striped jackal carcasses from	They found that 20% of recently post-partum female black-backed jackals had lost their entire litters (they had dry mammary glands). Average productivity was 1.5 pups per year per adult. They predict that 'only very severe culling would have

1846, and *Canis mesomelas* Schreber, 1778 (Carnivora: Canidae), in Zimbabwe. *African Zoology*, 37(1): 21-26.	rabies prevention operations in Zimbabwe 1990-96.	any long term effect on jackal populations' (2002: 25).
Bothma, J.D.P. 1971a. Control and ecology of the black-backed jackal *Canis mesomelas* in the Transvaal. *Zoologica africana*, 6(2): 187-193.	564 black-backed jackals killed by coyote getters between 1962 and 1969 in the Transvaal	More males than females, males heavier than females (1971: 191). Study found that most black-backed jackals were killed in the first two weeks after setting the getters and that kills became negligible after 2 weeks. Recommends that control efforts do not exceed two weeks.
Bothma, J.D.P. 1971b. Food of *Canis mesomelas* in South Africa. *Zoologica africana*, 6(2): 195-203.	378 stomach contents, mostly from the Transvaal	Males ate more food than females. Compared black-backed jackals in reserves and on farmlands. Carrion, rodents, hoofed domestic stock (particularly sheep) insects and hares were the most common food sources. 'Only 6.3% of stomachs from game reserves contained hoofed domestic stock, in contrast to 27.3% in agricultural areas' (1971: 999)
Brand, D.J., Fairall, N. & W.M. Scott. 1995. The influence of regular removal of black-backed jackals on the efficiency of coyote getters. *South African Journal of Wildlife Research*, 25(2): 44-48.	4 year study on the coast of the Northern Cape Province that used coyote getters to kill black-backed jackals.	It was found that the effectiveness of coyote getters declined over time and avoidance behaviour increased with regular control operations. Males were significantly more likely to be killed than adult females. This is attributed to individual learning, social exposure (seeing others die) and social learning (learning from behaviour of experienced black-backed jackals especially females who might have seen pups being killed by coyote getters).
Brassine, M.C. & D.M. Parker. 2012. Does the presence of large predators affect the diet of a mesopredator? *African Journal of Ecology*, 50(2): 243-246.	Analysis of scat and stomach contents of black-backed jackals in two protected areas in the Eastern Cape – one with large predators, the other without.	Mammals were found in 93% of scats in both areas. There was no significant difference in the overall diet or in the mammalian prey orders ingested between the two sites.

Deacon, F. (2010). Aspekte rakende die ruimtelike ekologie van die rooijakkals (Canis mesomelas) as probleemdier in die Suid-Vrystaat. (Unpublished M.Sc. dissertation). Bloemfontein, South Africa: University of the Free State. (In Afrikaans.)	Study area of 35 farms in the Free State.	Graph on page 22 showing the increase in numbers of black-backed jackals killed by the Tafelberg jag klub particularly in mid 2000s. On pages 30 and 31 he locates where the jackals were killed and breeding places – shows they are on ridges and hills, southern and eastern, with more vegetation (page 40). None were further than 500m away from water (page 50). Argues they are easy to control because they go back to the same places, they move their den sites not very far when disturbed, and if you have a non-problem animal, it is best to leave the pair undisturbed in order to prevent problem animals just moving in.
Do Linh San, E., Malongwe, N.B., Fike, B., Somers, M.J. and Walters, M., 2009. Autumn diet of black-backed jackals (*Canis mesomelas*) in the thicket biome of South Africa. *Wildlife Biology in Practice*, *5*(2), pp.96-103.	Great Fish River Reserve (no predators 'except anecdotal numbers of brown hyenas *(Hyaena brunnear*) and leopards (*Panthera pardus*))	Scat analysis of diet in the autumn (when there are newborn and older calves and lambs available. The diet of jackals from two areas of the reserve that differ in habitat structure and composition revealed a large and comparable food spectrum. The contribution of antelopes to jackal diet – expressed as relative volume of remains in the scats – reached 20.7%, followed by 'other mammals' (*Suidae*, *Tubulidentata*, *Primates*; 19.8%), arthropods (17.6%), rock hyraxes *Procavia capensis* and springhares *Pedetes capensis* (12.8%) and unidentified plant material (10.5%). Fruits, carnivores, small rodents and reptiles acted as supplementary food sources (18.6% in total).
Ferguson, J.W.H., 1978. Social interactions of black-backed jackals *Canis mesomelas* in the Kalahari Gemsbok National Park. *Koedoe*, *21*(1), pp.151-162.	Observational study in the Kalahari Gemsbok Park. Excellent photographs and diagrams	Social interactions of among black-backed jackals are amicable, agonistic and aggressive. Allogrooming within a pair is common and a fixed 'greeting' ceremony takes place between pair members. Agonistic postures and a repertoire of submissive behaviour indicate that black-backed jackals have a well-developed social life.
Ferguson, J.W.H., Nel, J.A.J. and De Wet, M.J., 1983. Social organization and movement patterns of Black-backed jackals *Canis mesomelas* in South Africa. *Journal of Zoology*, *199*(4), pp.487-502.	Studied social organisation and movement patterns in the Kalahari Gemsbok National Park and on farmlands.	Found that resident pairs tolerated other black-backed jackals at a water hole in their territory if submissive behaviour was displayed. Found evidence of helpers at dens. Recorded dispersals – found evidence to be in line with that of other wild canids demonstrating the drive to dispersal as being very strong (1994: 497). Cites two cases of black-backed jackal pups of different age in the same den, indicating that the helper gave birth and this could be a mechanism for compensating for high mortality on farmlands (1994: 499).

Forbes, R.W., 2012. The diet of black-backed jackal (*Canis mesomelas*) on two contrasting land-use types in the Eastern Cape Province, South Africa and the validation of a new analytical method of mammalian hair identification.	Black-backed jackal scat from Great Fish River Reserve and Shamwari private game reserve and two neighbouring live-stock farms (Eastern Cape). Manually and tested a program. From Nov 2009 to Oct 2010 on a monthly basis	Relative frequency of mammalian hair (33-47%) and vegetation (32-45%) dominating the diet throughout the year across the four study sites. Significant dietary shifts evident across seasons in the reserves but not the farms. More mammalian hair was present on the farms. There were less invertebrates in the reserves in winter and more fruit and seeds in autumn in the Great Fish River reserve. The mammalian component of the diet was dominated by ruminants and rodents on the game reserves and ruminants and livestock on the farms. Shows that jackals are opportunistic generalists.
Fourie, R.M., Tambling, C.J., Gaylard, A. and Kerley, G.I., 2015. Short-term foraging responses of a generalist predator to management-driven resource pulses. *African Journal of Ecology*, *53*(4), pp.521-530.	Scat analysis of dietary responses of black-backed jackals in the Karoo National Park to the reinforcement of springbok populations and then the reintroduction of lions	They show that black-backed jackals consumed more springbok after additional springbok were provided through a management intervention and that they consumed more ungulates (presumably carrion) after the lions were introduced into the park. They conclude that the key lesson is that the diet of generalist mesopredators is context dependent.
Hiscocks, K. and Perrin, M.R., 1987. Feeding observations and diet of black-backed jackals in an arid coastal environment. *S. AFR. J. WILDL. RES./S.-AFR. TYDSKR. NATUURNAVORS.*, *17*(2), pp.55-58.	Analysis of 47 scat of black-backed jackals on the Namibian coast (the Cape Cross Seal Reserve)	The main source of food was fur seals (86%) followed by birds (12%). Black-backed jackals were observed licking condensed fog off rocks and vegetation. They were opportunist scavengers and could rob gulls of their food. One jackal was observed killing a waterlogged cormorant. Black-backed jackals were observed caching food.
Hiscocks, K. and Perrin, M.R., 1988. Home range and movements of black-	Observational studies of black backed jackals at the	They argue that territoriality 'breaks down' in the presence of clumped resources, such as seal carcasses. They assume this because of large numbers of black-backed jackals on a carcass. NB

backed jackals at Cape Cross Seal Reserve, Namibia. *S. AFR. J. WILDL. RES./S.-AFR. TYDSKR. NATUURNAV.*, *18*(3), pp.97-100.	Cape Cross Seal Reserve	Jenner *et al* (2011) argue that territoriality is still evident because breeding pairs defend den sites.
Humphries, B.D., Ramesh, T., Hill, T.R. and Downs, C.T., 2016a. Habitat use and home range of black-backed jackals (*Canis mesomelas*) on farmlands in the Midlands of KwaZulu-Natal, South Africa. *African Zoology*, *51*(1), pp.37-45.	Five black-backed jackals were captured and GPS collared in farmlands in the KwaZulu-Natal midlands. They were tracked between May 2013 and September 2014.	Home ranges varied across seasons. Adult black-backed jackals preferred crop lands in the spring, summer and autumn and avoided them in winter. One male dispersed over 150 kilometres.
Humphries, B.D., Ramesh, T. and Downs, C.T., 2016b. Diet of black-backed jackals (*Canis mesomelas*) on farmlands in the KwaZulu-Natal Midlands, South Africa. *Mammalia*, *80*(4), pp.405-412.	Collected 154 black-backed jackal scat between May-August 2013 (winter) and January to March 2014 (summer) on farmlands.	They found 17 different prey items in summer and 19 different prey items in winter. Rodents were the dominant prey species (about half the total biomass) in both seasons. Domestic livestock (mainly cattle, unsurprising as this is predominantly cattle country) was also important (about a quarter of the biomass) – however the study could not distinguish between scavenging and kills. The authors have observed black-backed jackals hunting sick cattle and new born calves (page 5). NB – their 2015 study (below) showed that farmers often leave out carcases.
Humphries, B.D., Hill, T.R. and Downs, C.T., 2015. Landowners' perspectives of black-backed jackals (*Canis mesomelas*) on farmlands in KwaZulu-Natal, South Africa. *African Journal of Ecology*, *53*(4), pp.540-549.	Interviewed 59 commercial farmers in the Karkloof in 2012 most were cattle farmers.	There was a general perception that the number of black backed jackals had grown, particularly over the past ten years. They were regularly cited and caused occasional damage to livestock. They admitted to being part of the problem because only 41% buried dead livestock, the others left them for vultures (vulture restaurant 27%) or did nothing 32% (page 543).

Jenner, N., Groombridge, J. and Funk, S.M., 2011. Commuting, territoriality and variation in group and territory size in a black-backed jackal population reliant on a clumped, abundant food resource in Namibia. *Journal of Zoology*, *284*(4), pp.231-238.	Observational study at the Cape Cross Seal Reserve in Namibia.	Territories defended to 50 meters of the fur seal colony and displayed territorial behaviour around den sites. Group sizes increased with distance from the seal colony (they attribute this to helpers being beneficial for collecting food and carrying it back). They recorded 'jackal highways' – i.e. distinct paths through which black-backed jackals traversed the territories of others. They stuck to the trails and did not challenge those they passed.
Kamler, J.F., Foght, J.L. and Collins, K., 2010. Single black-backed jackal (*Canis mesomelas*) kills adult impala (*Aepyceros melampus*). *African Journal of Ecology*, *48*(3), pp.847-848.	Obervations at Moremi game reserve Okavango delta.	Black-backed jackal homed in on a healthy adult female impala and killed her after a long pursuit (exhausting the animal and then throttling it) – leaving the jackal exhausted. It rested, then ate some soft parts but lost the carcass to a hyena. They observe 'the energy required to successfully subdue the impala must have been considerable, thus it was unclear why the jackal engaged in this type of behaviour. That the carcass was usurped by a spotted hyena soon afterwards suggests this activity was not a good investment for the jackal' (2010: 848).
Kamler, J.F., Klare, U. and Macdonald, D.W., 2012. Seasonal diet and prey selection of black-backed jackals on a small-livestock farm in South Africa. *African Journal of Ecology*, *50*(3), pp.299-307.	Private sheep farm in the Free State Province (also some goats and cattle). Jackals persecuted. Scat analysis and transects to determine prey availability	Sheep were often the main source of food, fluctuating seasonally from 25-48%. Compared to the biomass available, jackals selectively consumed wild prey (especially mammals 1-3 kilograms) over sheep in most seasons. During spring, when both sheep and wild ungulates were birthing, jackals selectively consumed wild ungulates. During winter, when sheep but not wild ungulates were birthing, jackals selectively consumed the former over the latter. Thus jackals selectively consumed whatever group of ungulates was birthing and preferred wild ungulates (305)
Klare, U.N.N., Kamler, J.F., Stenkewitz, U.T.E. and Macdonald, D.W., 2010. Diet, prey selection, and predation impact of black-backed jackals in South Africa. *The Journal of Wildlife*	Two game ranches near Kimberly (elements of Savanna, Nama Karoo and Grassland). Large ungulates	Notes that jackals prey on gazelles, especially fawns, in East Africa and that this niche is filled by springbok (*Antidorcas marsupialis*) in Southern Africa. Diet was dominated by ungulates, mostly springbok, especially in the lambing periods in spring and autumn. Rodents consumed all year, but only in winter did it reach 11%. Also birds, insects, fruits, hares, springhares, small carnivores such as bat eared foxes and yellow mongoose. Medium sized mammals (hares

Management, *74*(5), pp.1030-1041.	intensively managed (hunting, culling) No apex predators. Scat analysis	and springhares) preferred over springbok. During lambing they feed exclusively on species that were hiders rather than followers (suggesting active preference and hunting for springbok rather than scavenging). Theory: they need more protein lactating and feeding pups, researchers found a lot of springbok fawn remains at jackal natal dens (1039). They recommend that jackals be seen as members of the large carnivore guild
Krofel, M., 2007. Opportunistic hunting behaviour of black-backed jackals in Namibia. *African Journal of Ecology*, *46*(2), pp.220-222.	Etosha National Park (Waterhole). 6 black-backed jackals	Observation of opportunistic attack on a springbok by a single jackal that was joined by other jackals in collaborative hunting. During eating, a status hierarchy was clear.
Loveridge, A.J. and Macdonald, D.W., 2003. Niche separation in sympatric jackals (Canis mesomelas and Canis adustus). *Journal of Zoology*, *259*(02), pp.143-153.	Hwange Estate (conservation area) in Western Zimbabwe, with safari camps. 11 side-striped and 11 black-backed jackals	Flexible and opportunistic diets, similar between species though black-backed jackals ate more springhares (and defended territory with springhares) and side-striped ate more safari camp refuse. Side-striped territories centred on human activity.
McManus, J.S., Dickman, A.J., Gaynor, D., Smuts, B.H. and Macdonald, D.W., 2015. Dead or alive? Comparing costs and benefits of lethal and non-lethal human–wildlife conflict mitigation on livestock farms. *Oryx*, *49*(04), pp.687-695.	A 'before and after' quasi experiment on 11 farms in the Eastern Cape where lethal control of black backed jackals occurred in the first year followed by two years on non-lethal methods.	Three farms received livestock guarding dogs, one received alpacas and the other seven received 'dead stop' (steel) livestock protection collars (2014: 3). In the year of lethal control, farmers lost on average 14.3 % of their stock. In the second year (i.e. the first year of non-lethal control) they lost an average of 4.4 percent of their stock, and in the third year 3.7 percent of their stock (*ibid*: 4). All farms experienced lower cost in the years of non-lethal control (*ibid*: 5). Follow-up after 13 months revealed that only 6 of the 11 farms continued to use non-lethal control (mostly those with guardian dogs) and the other five used a mixture of lethal and non-lethal methods. After 30 months after the end of the trial, only four of the original farms continued to use only non-lethal methods, five used a mixture of lethal and non-lethal and two had switched back to lethal control only (*loc.cit*). The authors conclude that non-lethal methods are cost-effective, but they fail to comment on why farmers increasingly switched back to including lethal-control in their arsenal over time. They accept that a limitation of their

		study was a lack of control farms (where lethal control was practiced for three years) but they do not acknowledge that the first year of lethal control may have reduced depredation in the second and third years.
Minnie, L., Gaylard, A. and Kerley, G.I., 2016. Compensatory life-history responses of a mesopredator may undermine carnivore management efforts. *Journal of Applied Ecology*, *53*(2), pp.379-387.	The authors studied black-backed jackal carcasses from culling operations between October 2011 and October 2013 in national parks in the Karoo and the Eastern Cape and on surrounding farmlands where these predators are heavily persecuted.	They found that culled black-backed jackals were younger on the farms, had a lower age of first pregnancy and larger litter sizes. They conclude that hunting on farms changed population dynamics, from a stable to an expanding population and that 'source-sink' dynamics were probably evident, that is dispersal from source areas like the national parks to farmlands. The paper neglected to mention that there was an earlier cull in 2010 in the national parks (which could well have affected population characteristics) and the study assumed that there was no behavioural differences between the way that black-backed jackals responded to call and shoot culling operations in the national park (where this happens rarely) and on farms (where this happens regulations). This is potentially of concern given that black-backed jackals become wary of lethal control measures and that juveniles will be more easy to kill on farms than adults.
Moehlman, P.D., 1979. Jackal helpers and pup survival. *Nature*, vol.277: 382-3.	Serengeti (national park). 15 litters of black-backed jackals, nine pairs	In four out of five black-backed jackal families observed with consecutive litters, some of the previous year's litters stayed on as helpers, catching and regurgitating food and protecting the pups when adults were away. Each helper added 1.5 surviving pups to the litter. The presence of helpers was unrelated to the food supply. Helpers promote inclusive fitness.
Moehlman, P.D., 1987. Social organization in jackals: the complex social system of jackals allows the successful rearing of very dependent young. *American Scientist, 75*(4), pp.366-375.	Serengeti (national park)	This paper is a readable summary of 12 years of research on black-backed jackals and golden jackals in the Serengeti. It argues that helpers are important for pup survival, especially amongst black-backed jackals that depend on rodents during the breeding season (whereas golden jackals depend on fawns during the breeding season). She argues that male investment is consequently more important in black backed jackals and pair bonds are thus stronger.
Rowe-Rowe, D.T., 1975. Predation by black-backed jackals in a sheep-farming region of Natal.	Study of impact of predation on five sheep farms in Natal.	Natal Parks Board hunted black-backed jackals between 1953 and 1971 at which point it was decided to conduct research on the impact of black-backed jackals on farms. Predation to black-backed jackals was deemed to be responsible for

South African Journal of Wildlife Research-24-month delayed open access, *5*(1), pp.79-81.		the loss of 0.05% of sheep and that most losses were in the dry season (winter and spring) when the sheep were lambing and hunting dog packs were less effective at killing jackals. Recommended that farmers invest in more protective methods, like fences.
Rowe-Rowe, D.T. (1982). Black-backed jackal diet in relation to food availability in the Natal Drakensberg. *South African Journal of Wildlife Research*, 13, 17–23.	Scat analysis in Giant's Castle Game Reserve, together with camera trap study	Found that the black-backed jackal was primarily a searcher, living on the most abundant, conveniently sized prey; and a pursuer or scavenger only opportunistically.
Stuart, C.T., 1976. Diet of the black backed jackal *Canis mesomelas* in the central Namib Desert, South West Africa. *Zoologica Africana*, *11*(1), pp.193-205.	Namib desert park Namibia (coastal, dry riverine, open plains). Scat analysis	Confirms that jackals are opportunistic feeders, when on the coast their diet was mainly bird and marine waste, they consumed seeds and fruit when available, rodents, insects, reptiles. They also ate carrion.
Van de Ven, T.M., Tambling, C.J. and Kerley, G.I., 2013. Seasonal diet of black-backed jackal in the Eastern Karoo, South Africa. *Journal of arid environments*, *99*, pp.23-27.	Samara Private Game Reserve, Eastern Cape. 240 black backed jackal scats	Ungulates (mostly small) were the dominant prey item across all seasons – the stability being facilitated by scavenging opportunities most likely provided by cheetahs. Rodents and medium mammals were also consumed though these varied more across the seasons.

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