Causes of mortality in a population of black-footed cats in central South Africa

Running head: Black-footed cat mortality in South Africa

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1 | INTRODUCTION

Mortality influences population dynamics and may affect a species' potential for survival. Identifying the primary causes of mortality of a species is therefore essential to understand population ecology, but is also important from a management and conservation perspective (Ruggiero, Hayward, & Squires, 1994). The relative frequency of the various causes of mortality within a population provides information about local ecology, evolutionary pressures and reveals potential conservation issues (Collins & Kays, 2011). The knowledge of cause-specific mortality is particularly relevant for endangered species, considering one of the most important actions to reverse a species' decline is to mitigate the most significant causes of mortality through targeted efforts (Angerbjörn et al., 2013; Simón et al., 2012).

In both large and small wild cats, the majority of mortalities are often directly or indirectly human-related, with the main causes of death including hunting, poaching, retaliatory killing, vehicular collision, predation by domestic dogs and infectious diseases transmitted from domestic animals (Andrén et al., 2006; Blankenship, Haines, Tewes, & Silvy, 2006; Goodrich et al., 2008; Gubbi, Poornesha, Daithota, & Nagashettihalli, 2014; Pereira et al., 2010; Schmidt-Posthaus, Breitenmoser, Posthaus, Bacciarini, & Breitenmoser, 2002). In addition, small wild cat species are often subject to lethal encounters with larger competitors. For example, pumas (*Puma concolor*) were the main cause of mortality of Geoffroy's cats (*Leopardus geoffroyi*) in a national park (Pereira et al., 2010) and raptors and red foxes (*Vulpes vulpes*) accounted for 41% of deaths in Pallas's cats (*Otocolobus manul*; Ross, 2009). Diseases and intraspecific mortality were also important causes of mortalities in Iberian lynx (*Lynx pardinus*; López et al., 2014) and ocelots (*Leopardus pardalis*; Haines, Tewes, & Laack, 2005).

The black-footed cat (*Felis nigripes*) is the smallest felid species in Africa and endemic to the arid regions of southern Africa. It is currently listed as "Vulnerable" in the International Union for the Conservation of Nature (IUCN) red list of threatened species, with a population decline suspected over the general range (Sliwa, Wilson, Küsters, & Tordiffe, 2016). Since 2005, the Black-footed Cat Working Group has been conducting long-term monitoring of black-footed cats in two study areas in South Africa. In this study, we used data from radio-collared animals to evaluate the relative importance of the different causes of mortality in this population.

2 | METHODS

2.1 | Study areas

The study areas were located in the central part of South Africa (Fig. 1). The first study area is Benfontein Nature Reserve (28°50'S, 24°50'E), a Natural Heritage Site owned by De Beers Consolidated Mines, located 10 km south-east of Kimberley on the border of the Northern Cape and Free State Provinces. The 114-km^2 reserve is composed of semi-open savannah and dwarf shrubland. The second study area covers Nuwejaarsfontein (30°50'S, 24°01'E) and Taaiboschpoort Farms (30°57'S, 24°00'E), mixed sheep and game farms adjacent to each other located 24 km south of De Aar in the Northern Cape Province. The 90-km^2 Nuwejaarsfontein Farm and 45-km^2 Taaiboschpoort Farm are composed of Karoo plant communities. The only two potential black-footed cat predators in both study areas are the caracal (*Caracal caracal*) and the black-backed jackal (*Lupulella mesomelas*, jackal hereafter). Leopards (*Panthera pardus*) are rarely observed and never remain for more than a few days. Game managers keep their domestic dogs under their supervision and, on rare occasions, shot any feral dogs that had entered the properties. Use of rodenticides does not occur in both study areas.

2.2 | Data collection and analysis

Black-footed cats were captured using nets, digging or baited traps as described in Sliwa (2004) and immobilised as detailed in Eggers et al. (2020). Captures were conducted once a year from 2005 to 2020 on Benfontein and from 2009 to 2018 on Nuwejaarsfontein and Taaiboschpoort. Upon capture, sex and age class (adult, sub-adult and kitten) of cats were determined as described in Sliwa (2004, 2006). Only adults and sub-adults weighing ≥ 1 kg were fitted with small custom-built radio-collars (Advanced Telemetry Systems Inc, Isanti, MN, USA) with a mortality switch, weighing 42-60 g.

Capture and handling methods were approved by the Northern Cape Department of Environment and Nature Conservation (permit number: FAUNA 1218/2016). Tracking frequency varied throughout the years, but was conducted at least once a month on average. Visual contact with individuals and behavioural observations were carried out regularly as part of long-term monitoring and collection of home range data. Cats found dead during routine monitoring or after a mortality signal was detected had their carcasses and surroundings inspected to determine cause of death. If the carcass was relatively fresh, a necropsy or histopathological analyses on formalin-fixed tissue samples, or both, were performed at the Faculty of Veterinary Science of the University of Pretoria. Samples consisted of both kidneys, liver, spleen and adrenal glands (if abnormal in size and shape). Considering that the head circumference of black-footed cats is distinctly larger than the neck circumference, it was highly unlikely that a live cat could slip its collar. Therefore, if only the collar was found, the cat was considered to be dead.

Causes of mortality were classified as (1) natural causes, (2) human-related causes, or (3) undetermined causes. (1) Natural causes included intraguild killing by larger carnivores (presence of blood, puncture and bite marks on carcass or collar, see below), diseases (based on either necropsy, histopathological analyses, or both, but see below), burrow collapse (carcass found in a collapsed burrow) and unknown natural causes (complete and untouched carcass but specific cause, e.g. disease or starvation, could not be determined). Based on wounds inflicted (Stuart & Stuart, 2013), deaths due to intraguild killing were attributed to caracal or jackal. Caracals leave characteristic canine puncture marks without consuming any flesh, while jackals usually leave bite marks on

the collar, tear the body in pieces and possibly partly consume it. Considering jackals are also scavengers, there remains some uncertainty regarding the cause of death when involving jackals. However, the probability of jackals finding a carcass of a dead cat should be relatively low, due to the small size of the carcass and the relatively large home ranges of jackals. In some cases, behavioural observations of collared individuals in the field suggested a disease state prior to death (Fig. 2). Since healthy black-footed cats get hydration from their prey and rarely drink water (Sliwa, 2013), observing frequent drinking (at least once a night), as well as movements becoming restricted near permanent surface water, indicated that kidney function in the cat was compromised. Indeed, increased water intake is usually a relatively reliable clinical sign of kidney disease in small felids, such as the domestic cat (*F. catus*; Bartlett, Van Buren, Bartlett, & Zhou, 2010). These atypical behaviours were sometimes accompanied by signs of deteriorating body condition, such as weight loss, scruffy fur, lethargy or infrequent grooming (Zimmermann, Lawrenz, & Sliwa, 2011). We classified animals presenting these behaviours and clinical signs prior to their deaths as a suspected renal disease associated-mortality ("suspected renal failure") when the state of carcasses prevented a gross necropsy and histologic diagnosis. (2) Human-related causes could involve any deliberate or accidental killing of a cat by people. (3) Undetermined cause was attributed when the cause of death could not be assessed from the remains (i.e., the carcass was already too decomposed or only the collar was found).

3 | RESULTS

A total of 59 cats were radio-collared (26 females, 33 males) during the study period. Mean monitoring duration was 16.5 ± 14.5 months, ranging from two weeks to up to five years depending on the individual. A total of 38 death events (18 females, 20 males) were recorded, with 23 on Benfontein and 15 on Nuwejaarsfontein/Taaiboschpoort (Table 1). Although all cats were captured in the study areas, eight (21%) individuals were found dead outside their limits. Fourteen carcasses were found within 1-4 days after death, while 24 were found one week or more after death.

The cause of death could be determined in 25 cases (66%), leaving 13 cases undetermined (34%). The main causes of mortality were intraguild killing (11 cases, 29%) and diseases (six cases, 16%), followed by unknown natural causes (four cases, 11%), burrow collapse (two cases, 5%), and human-related causes (two cases, 5%). Black-footed cats were killed by jackals in six cases and by caracals in five cases. Detected diseases included renal failure due to AA amyloidosis (three cases), suspected renal failure (two cases) and pneumonia (one case). In the four cases of unknown natural causes, two cases involved emaciated bodies found without prior clinical signs of disease during a prolonged drought period (potentially starvation, or undiagnosed diseases). Regarding human-related mortalities, one cat was killed by farm labourers. As the animal was displaying disoriented behaviours near a water trough, farm staff assumed it was infected with the rabies virus and killed it by trauma to the head with a rock. This cat was diagnosed with renal failure post mortem and AA amyloidosis was confirmed histologically. The other cat, also presenting clinical signs of renal failure before death, was found with its head cut off on a neighbouring farm. The clean-cut mark on the head suggested human-related circumstances such as snaring (possibly accidental).

4 | DISCUSSION

This study identified intraguild killing, as well as diseases, particularly renal failure most probably associated with AA amyloidosis, as the two most important causes of mortality affecting black-footed cats in central South Africa. Determining the exact cause of deaths in warm climate regions remains difficult. Indeed, despite regular monitoring by radio telemetry and observations, causes of death could not be determined for about one third of cases mainly due to rapid decomposition, sometimes even when the carcass was found within a day. Nevertheless, contrary to the situation in most small cat species, mortalities of black-footed cats in our study areas were mostly attributed to natural causes rather than human-related causes. This may not be surprising since cats were monitored on private properties with the permission and support of land owners. Often, some cats also crossed over to other neighbouring properties without experiencing direct or indirect human-caused fatalities (except for two). While the black-footed cat is a protected species across most of its range (Sliwa et al., 2016), as observed in guignas (*Leopardus guigna*; Sanderson, Sunquist, & Iriarte, 2002) and fishing cats (*Prionailurus viverrinus*; Chowdhury, Chowdhury, Ahmed, & Muzaffar, 2015), legal protection does not necessarily prevent persecution and illegal killings as retaliation for depredation of small livestock. The low number of human-caused deaths in this study may therefore indicate a low human-predator conflict when involving black-footed cats and a high tolerance level towards the species in the region. Positive public perception is important for human-felid coexistence (Inskip & Zimmermann, 2009). It should however be noted that, although not encountered in this study, several instances of accidental killings of black-footed cats by

vehicular collision or during lethal control of other managed carnivores have been reported elsewhere (Sliwa et al., 2016; Küsters, in review; Wilson, 2015).

4.1 | Intraguild killing

Intraguild killings are common in carnivores (Palomares & Caro, 1999), although their purpose is not completely understood (Bertin, 2019; Curveira-Santos et al., 2022; Donadio & Buskirk, 2006). So far, although consumption of the victim after aggression sometimes occurs, the "predatory killing hypothesis" (intraguild killing being conducted for energetic gains obtained through predation) has received little empirical support. Research has supported the "resource overlap hypothesis" (also called "competitive killing hypothesis": intraguild killing is predominantly performed to reduce exploitation competition, especially over food resources), but only to some extent (but see Bertin, 2019; Donadio & Buskirk, 2006). Recently, Bertin (2019) suggested a greater role of non-competitive killing with the "incidental killing hypothesis", which states that non-adaptive (neutral) killing interactions may occur when costs of engaging in the killing are low. Lethal interactions are undertaken mainly by predaceous species that are highly adapted to kill (i.e., specialised dentition) and become more common when the killer species is 2 to 2.5 times the mass of the victim (Bertin, 2019; Donadio & Buskirk, 2006). On Benfontein, black-backed jackals regularly kill black-footed cats, Cape foxes (*Vulpes chama*) and bat-eared foxes (*Otocyon megalotis*), despite a minimal diet overlap amongst these species (Kamler, Stenkewitz, Klare, Jacobsen, & Macdonald, 2012; Kamler et al., 2015). Since killing events mostly occur during the pup rearing season (Kamler et al., 2012), presence of pups may exacerbate territorial aggressivity of jackals, leading to higher incidence of intraguild killing seasonally. Jackals killing black-footed cats may

therefore support the “incidental killing hypothesis”. But considering incidental aggression and opportunistic predation are not mutually exclusive (Curveira-Santos et al., 2022), cats killed and then consumed by jackals may also represent opportunistic predation. Furthermore, felids are most often killed by other felids, which was suggested to be linked to felids’ hyperpredatory lifestyles (Bertin, 2019). In line with other reports of felids killing sympatric carnivores (Helldin, Liberg, & Glöersen, 2006; Koehler & Hornocker, 1991; Sunde, Overskaug, & Kvam, 1999), caracals did not consume their black-footed cat victims. Caracals may have a larger dietary overlap with black-footed cats than jackals, since micromammals often constitute an important part of their diet (Braczkowski et al., 2012; Drouilly, Nattrass, & O'Riain, 2018). More research is needed to determine if killing of black-footed cats by caracals fit the “resource overlap hypothesis” or the “incidental killing hypothesis”. Besides the purposes behind carnivore intraguild killing, it is essential to assess the consequences of this source of mortality on the abundance of black-footed cat populations.

4.2 | Renal failure and AA amyloidosis

Amyloidosis is a disease resulting from abnormal folding of proteins which are deposited as fibrils in organ tissues (typically the kidney, liver, spleen and lymph nodes) and disrupt normal organ function. AA amyloidosis refers to the deposition of the A-amyloid protein and is the most common type found in mammals and birds, usually leading to death from hepatic or renal failure (Terio, O'Brien, Lamberski, Famula, & Munson, 2008; Woldemeskel, 2012). Captive black-footed cats are known to be particularly susceptible to renal failure and AA amyloidosis is the most common cause (Terio et al., 2008). The species appears to be genetically predisposed to AA amyloidosis (Terio et al., 2008). If

not directly causing death, renal failure may also weaken affected individuals and make them more likely to encounter predators or humans in a vulnerable state. Indeed, two cases of killings by jackals on Benfontein and both human-related deaths (one near Benfontein and one near Taaiboschpoort Farm) involved cats that were showing clinical signs of renal disease. While cats affected by renal failure were observed on both sites, a low intensity of predator (jackal and caracal) control on Benfontein may lead to a higher predator density (and hence higher encounter rate) on that site compared to Nuwejaarsfontein/Taaiboschpoort Farms, which may explain why we did not find cats that had died only as a result of renal disease on Benfontein (affected cats get killed before dying of the disease). In captive black-footed cats, AA amyloidosis has been associated with chronic stress and increased levels of the serum A amyloid (Terio et al., 2008). Stress associated with displacement out of home range (n = 4) and dispersal outside study areas (n = 3) could have exacerbated disease progression. Considering the high incidence of AA amyloidosis in black-footed cats in captivity (Terio et al., 2008) and potentially in the wild (Zimmermann et al., 2011; this study), investigating the underlying genetic factors and potential transmission mechanisms of AA amyloidosis in this species will be crucial for its conservation. Future studies should focus on whether stress, caused by physiological, social and environmental, is a contributing factor for the development of amyloidosis in wild black-footed cats.

4.3 | Management implications

The antagonistic interactions between black-footed cats and other carnivores are a cause of concern, but underscore a complex issue. In South Africa, both caracals and jackals are considered major predators of small livestock and subjected to lethal control (Tensen,

Drouilly, & van Vuuren, 2018). Judicious predator control for livestock protection may be beneficial for black-footed cats ("mesopredator release hypothesis", Crooks & Soulé, 1999). Indeed, the presence of dominant predators can cause low population densities, declines or even extirpation of smaller and less competitive species (Linnell & Strand, 2000; Oliveira et al., 2010). However, despite > 350 years of persecution, jackals and caracals have been relatively resilient to lethal management. In response to high population turnover, compensatory immigration was observed in both species (Minnie, Gaylard, & Kerley, 2016; Tensen et al., 2018) and compensatory reproduction was reported in jackals (Minnie et al., 2016). Non-lethal techniques, such as selective exclusion fences, may potentially be more efficient as a management tool for predator control, but more research should be conducted to address these issues. Alternatively, the presence of a healthy community of fossorial species, like springhares (*Pedetes capensis*), is probably beneficial for persistence and survival of black-footed cats, since burrows help them escape predators (Kamler et al., 2015; Wilson, 2015). However, this underscores another human-wildlife conflict since springhares are often killed to prevent damage caused by their burrows, or are harvested as bushmeat (Wilson, 2015). Concurrently, the mortalities associated with renal failure attributed to AA amyloidosis and the species' genetic predisposition to this disease raise concerns regarding habitat fragmentation and subsequent genetic isolation of subpopulations that could increase its prevalence.

Causes of mortality may change over time depending on several factors, such as increased human development, critical habitat loss, or improved species awareness (Chowdhury et al., 2015; Marker, Mills, & Macdonald, 2003). This dataset on the causes

of mortality in black-footed cats highlights the importance of long-term studies and complete post-mortem examination with histology for a better understanding of a species' ecology and will also provide a baseline for future comparisons.

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DATA AVAILABILITY STATEMENT

The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

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TABLE

TABLE 1. Causes of mortality of radio-collared black-footed cats monitored on Benfontein Nature Reserve (2005-2021) and Nuwejaarsfontein/Taaiboschpoort Farms (2009-2018) in central South Africa. Numbers in square brackets indicate the number of individuals that showed clinical signs of renal failure prior to death but ultimately died from a cause other than disease (all individuals in the category "Diseases" showed clinical signs of disease in the field prior to death).

Causes of mortality	**Benfontein**		**Nuwejaarsfontein/ Taaiboschpoort**	
	Female	Male	Female	Male
Intraguild killing				
Killing by caracal	2	2	1	
Killing by jackal	1	4 [2]	1	
Diseases				
Renal failure due to AA amyloidosis			1	2
Suspected renal failure			1	1
Pneumonia		1		
Other natural causes				
Burrow collapse	1	1		
Unknown natural cause			3	1
Human-related cause				
Killing by humans		1 [1]		1 [1]
Undetermined causes	5	5	2	1
Total	**9**	**14**	**9**	**6**

FIGURE LEGEND

FIGURE 1. Location of study areas, Benfontein Nature Reserve (10 km south-east of Kimberley) and Nuwejaarsfontein and Taaiboschpoort Farms (24 km south of De Aar), Northern Cape province, South Africa.

FIGURE 2. Wild black-footed cat "Stan" (male) initially captured on Nuwejaarsfontein Farm, here photographed shortly before death near a puff adder (*Bitis arietans*), had been showing clinical signs of disease for several months and was diagnosed with renal failure due to AA amyloidosis post mortem. Photo credits: Martina Küsters.

FIGURES

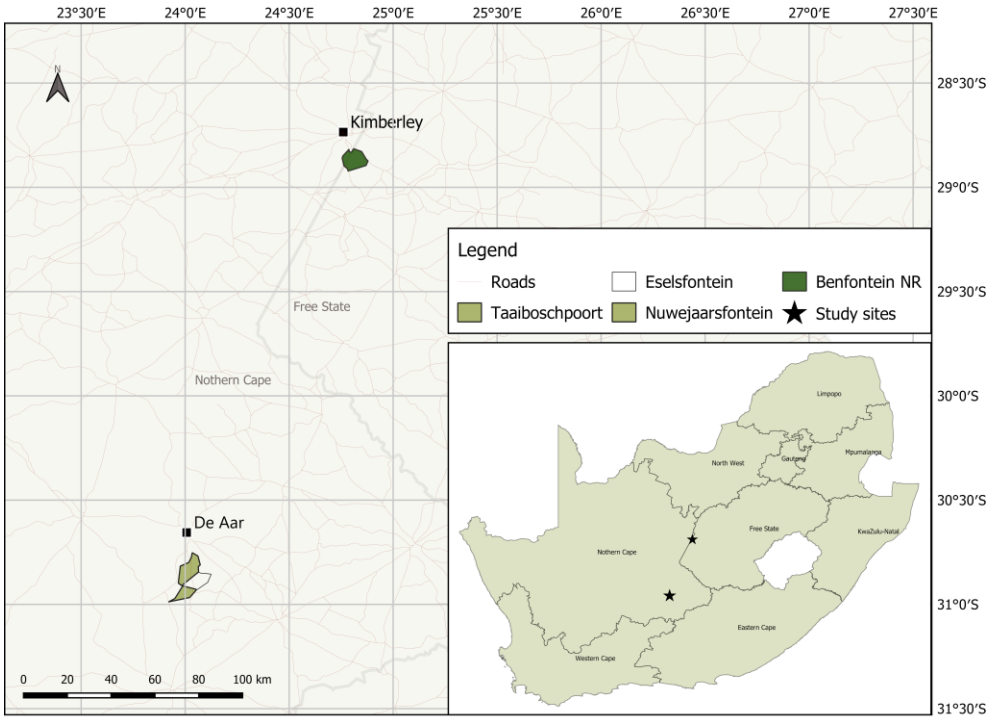

FIGURE 1

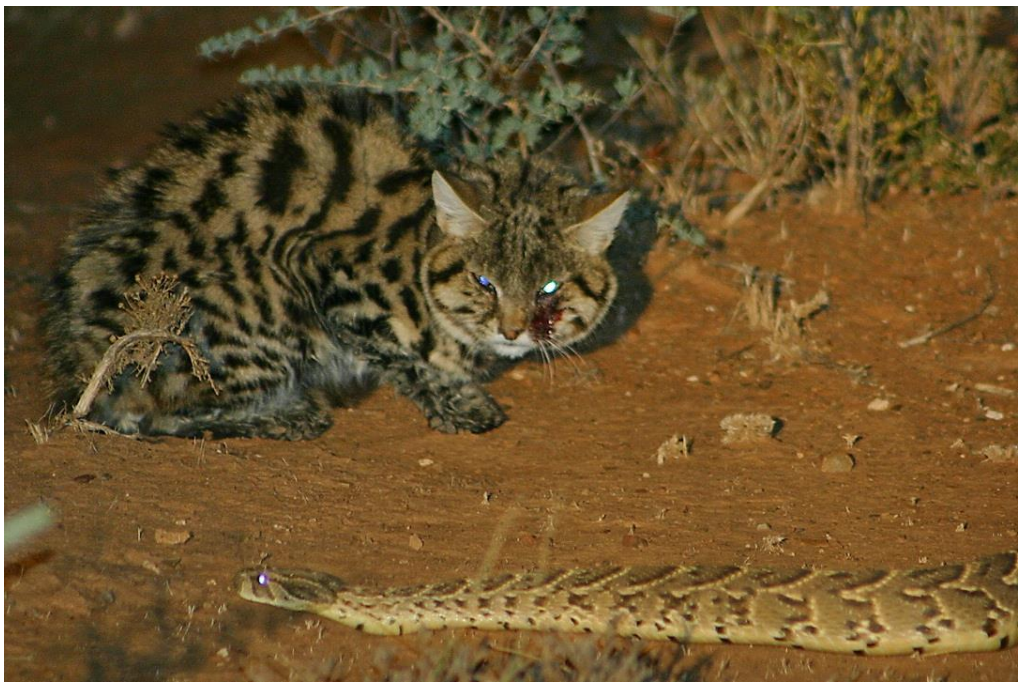

FIGURE 2