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Source: Journal of Vertebrate Biology, 69(3)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: <https://doi.org/10.25225/jvb.20033>

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# Investigating the hidden costs of livestock guarding dogs: a case study in Namaqualand, South Africa

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► Received 30 March 2020; Accepted 7 May 2020; Published online 6 July 2020.

**Abstract.** The use of livestock guarding dogs (LGDs) has been widely advocated as a responsible tool for reducing livestock predation and conserving wildlife. However, their hidden ecological costs have rarely been investigated. We analysed scats ( $n = 183$ ) from six LGDs and visited Global Positioning System (GPS) location clusters ( $n = 352$ ) from nine GPS-collared LGDs to reconstruct their diet and assess impacts on wildlife and livestock in Namaqualand, South Africa. Wild mammals, including 10 native species, and small-livestock were the main secondary foods (i.e. besides dog food pellets). A total of 90% of scats and one third of GPS clusters investigated had associated animal remains. When accompanied by a human attendant, fewer LGD scats contained animal matter (39.9%; of which 32.3% wild mammals and 4.6% livestock), in contrast to scats of LGDs on their own (93.2%; 14.4% wild mammals, 75.4% livestock). Similarly, few clusters of accompanied LGDs included animal remains (5.7%; of which 43.8% wild mammals and 31.3% livestock), whereas unaccompanied dogs clustered frequently at carcasses (92.4%; 16% wild mammals, 74% livestock). While sample sizes were relatively small and some dogs might have scavenged, we emphasize the importance of rigorous training and intensive monitoring of LGDs to correct unwanted predation behaviour and to maximize their ecological and protective benefits.

**Key words:** Anatolian shepherd dog, depredation, diet, Ecoranger, GPS cluster, livestock predation

## Introduction

Interactions between carnivores and humans in the form of competition for resources are widespread worldwide and can result in livestock predation by carnivores (Torres et al. 2018) and retaliatory killing of predators by farmers (van Eeden et al. 2018). This ancient conflict is one of the leading causes of mammalian carnivore declines worldwide and predator control is one of the oldest forms of wildlife

management (Berger 2006). While traditionally considered the most economical and effective method, increasing evidence suggests that lethal control can fail to mitigate depredation in the long-term, and at times may even be counterproductive (Minnie et al. 2016, Teichman et al. 2016, Treves et al. 2016, Nattrass et al. 2019). Unselective lethal control methods are also considered by some as inhumane because they can cause suffering, as well as injury and mortality to non-target animals

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including domestic animals, protected species, and other wildlife (Naughton-Treves & Treves 2005, Rochlitz et al. 2010). Such criticisms have raised ethical concerns and public opposition to lethal control programs is growing (Arthur 1981, Reiter et al. 1999, Slagle et al. 2017).

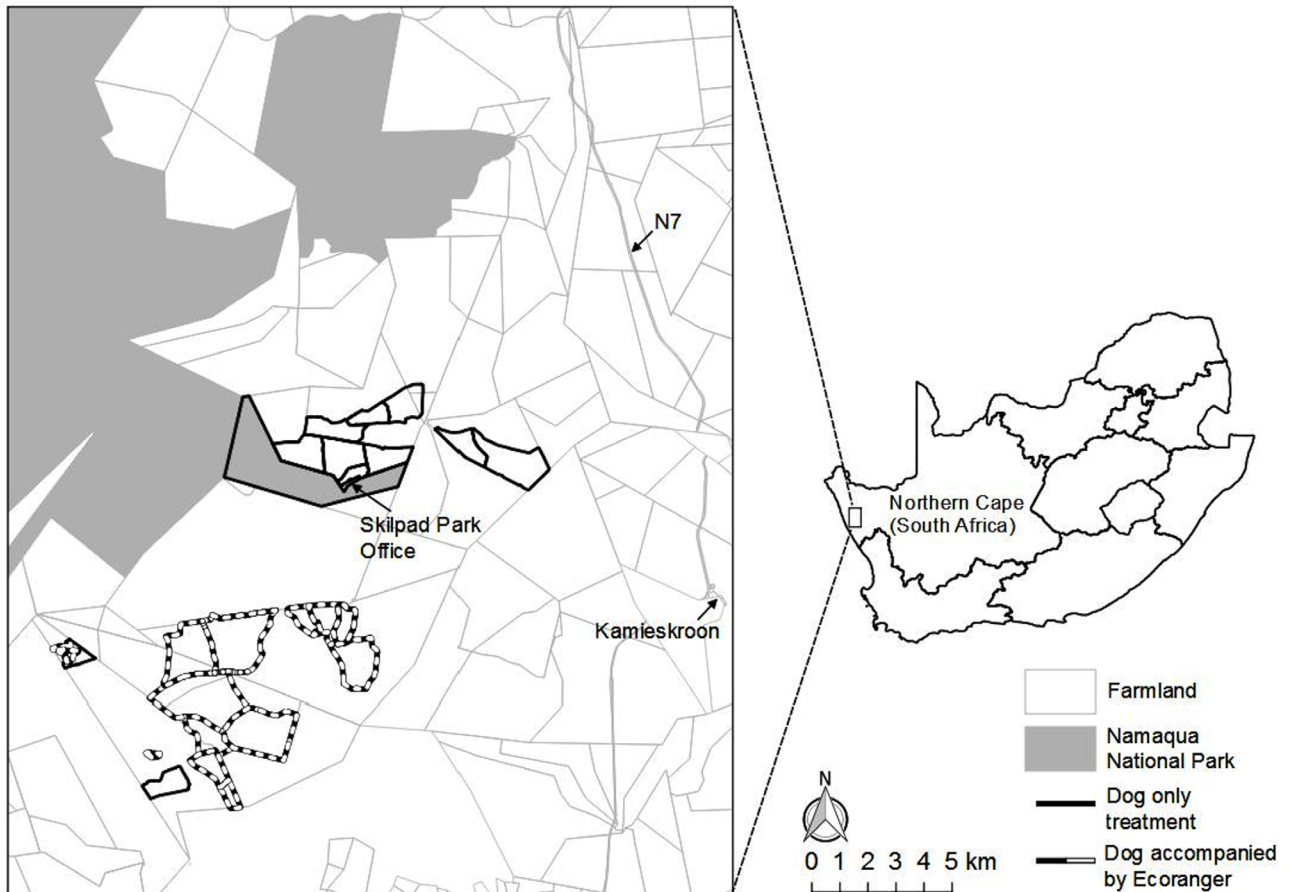
Nonlethal or selective predator management by contrast are gaining traction because they can address many of these concerns while seeking to maintain the vital role carnivores play in natural ecosystems. One of the most widely acclaimed selective predator management methods is the use of livestock guarding dogs (LGDs) (van Eeden et al. 2018). A review by Smith et al. (2000) on the efficacy of LGDs in North America and Europe reports that guarding animals can reduce small-stock depredations by 11-100%. In South Africa they have been shown to reduce predation by 68-100% (Rust et al. 2013), which, if applied across entire farming regions, could significantly alleviate depredation rates and thus farm productivity. LGDs have the benefit of serving as both a primary repellent (disruptive stimulus) and secondary repellent (aversive stimulus), with the potential to change carnivore behaviour (Gehring et al. 2010). Two recent studies have shown that LGDs may protect small-livestock without excluding carnivores from guarded farms (Allen et al. 2017, Spencer et al. 2020), which further validates their use as an effective dual conservation and protection tool. However, LGDs (such as the Anatolian shepherd dogs used in this study) might also function as an introduced carnivore preying on both wildlife and livestock. The lethal and nonlethal costs of their presence on both livestock and wildlife have been largely overlooked (Timm & Schmitz 1989, Potgieter et al. 2016) and it has even been proposed that LGDs could have more undesirable welfare implications for wildlife than traditional control methods (Allen et al. 2019).

While feral dogs have been shown to be ecologically disruptive and able to cause ecosystem-wide disturbances through predation (Feldmann 1974, Young et al. 2011), LGDs have been selectively bred to encourage traits that protect livestock and minimize hunting (Smith et al. 2000). Despite these precautions, anecdotal accounts exist of LGDs chasing and killing non-target wildlife (Timm & Schmitz 1989, Casey et al. 2005, Marker et al. 2005a, b, Gingold et al. 2009, Potgieter et al. 2013, 2016) with concomitant adjustments in behaviour and habitat use by wildlife (Gingold et al. 2009, van Bommel & Johnson 2017). In Turkey, Anatolian shepherd dogs

have been documented killing wolves (Urbigkit & Urbigkit 2010). One study based on farmer-reported LGD-wildlife interactions for 225 LGDs on South African farms revealed that 71 dogs (32%) were involved in such interactions, particularly with predators (73%) (Whitehouse-Tedd et al. 2020). Another study of 83 LGDs conducted in Namibia found that 53% of the dogs killed predators, and 18% of the dogs killed prey species (Potgieter et al. 2016). In the latter study, farmers and dogs combined killed more of the main small-livestock predator, the black-backed jackal (*Canis mesomelas*), than the farmers did before the dogs were introduced.

Currently, most studies concerning the effectiveness of LGDs and their interactions with wildlife rely solely on farmer recollections, reports and anecdotes (Green et al. 1984, Marker et al. 2005a, b, Potgieter et al. 2013, 2016, Leijenaar et al. 2015, Whitehouse-Tedd et al. 2020). While livestock producers may faithfully report their observations (Conradie & Nattrass 2017), such qualitative data are problematic for several reasons. First, potential carcass remains are notoriously difficult to locate in the field, possibly leading to underestimation of LGD impacts on wildlife and livestock (Lindzey & Wilbur 1989, Stoddart et al. 2001). Once located, carcasses are rarely found in good enough condition to determine the cause of death (Linnell et al. 2012, Conradie & Nattrass 2017). While many farmers claim they can differentiate between signs of predation, few if any record this information, necessitating reliance on long-term recollection (Marker et al. 2005a, Conradie & Nattrass 2017). Together, this over reliance on unverifiable reports has prompted the scientific community to prioritize empirical assessments for evaluation of this predation management tool (Gehring et al. 2010, Thorn et al. 2012, Potgieter et al. 2016, Treves et al. 2016, Eklund et al. 2017).

In South Africa, more than 300 LGDs have been placed on farmlands to defend livestock from carnivores (Stannard & Cilliers 2018). In the Northern Cape Province of South Africa, 90% of farmers practice lethal control (van Niekerk 2010). However, nonlethal measures are also used, with 87% of farmers reporting the use of at least one nonlethal control method (van Niekerk 2010) and 4% using LGDs (van Niekerk 2010). In this study, we investigated the diet of nine Anatolian shepherd dogs used as LGDs on commercial small-livestock farms in the Namaqualand region of the Northern Cape Province of South Africa. We used two different methods, scat analysis and GPS location



**Fig. 1.** Map of the study area in the Northern Cape Province of South Africa. The boundaries of different farm sections on commercial small-livestock farms are represented by grey lines. Camps with dogs only are delineated by black lines and camps with dogs accompanied by Ecorangers are delineated by black and white lines. The Namaqua National Park is in grey shading, with the Skilpad section of the park used periodically by a sheep flock.

cluster visitation, to investigate whether LGDs consume wildlife, including native species, as well as livestock. We separated our results according to two treatments: LGDs accompanied by a human attendant (Ecoranger), and LGDs guarding livestock on their own. Based on our review of the literature, we predicted that 1) LGD diets would include some wildlife and domestic species, and 2) that LGDs guarding on their own would consume more wildlife and livestock than those accompanied by an Ecoranger. Our study provides insight into the relationship between LGDs, Ecorangers and the wild and domestic species that share the landscape. The information documented herein contributes to a growing understanding of the secondary effects of methods traditionally classified as nonlethal predator management.

## Material and Methods

### Study area

This study was conducted on four free-ranging small-livestock commercial farms surrounding

the Namaqua National Park (30°2'36 S, 17°35'10 E) as well as the Skilpad section of the park, in South Africa's Northern Cape Province (Fig. 1). The study area falls within the Succulent Karoo biome that is recognized as a biodiversity hotspot, with more than 3,500 plant species, of which over 1,000 are endemic (Driver et al. 2003). Classified as a winter rainfall region, annual precipitation ranges from 178-263 mm (Cowling et al. 1998) and temperatures range from 5 °C in winter months (June-July) to 30 °C during summer. The elevation of the study area spans 354-825 m. Depredation levels were reportedly (farmers pers. comm.) high in the study area, and attributed to black-backed jackal, caracal (*Caracal caracal*), which was the most abundant predator, leopard, which were rare on target farms, and chacma baboon (*Papio ursinus*) (B. Cristescu, K. Teichman pers. comm.; Jansen et al. 2019). Intensive non-selective mesopredator removal occurred on farmlands, but nonlethal management methods to prevent predation were also used by farmers and included jackal-proof fencing (a wire mesh fence approximately 1.3 m



high packed with rocks at the bottom to discourage animals from digging underneath), electrified fencing, livestock rotation and fence patrols. These fences also prevented any encounter between the LGDs and livestock other than the ones they were guarding. Lethal management did not occur in farm areas where study flocks were protected by LGDs (see details below).

### Livestock study flocks and livestock guarding dogs (LGDs)

The four study farms comprised grazing camps separated by livestock fencing (multi-strand wire) that did not impede predators or most wildlife species. Focal study flocks of sheep or goats were rotated through camps to minimize grazing impacts on vegetation. The type of livestock flock has been shown to have little influence over the effectiveness of LGDs in South Africa (Leijenaar et al. 2015), however, anecdotal accounts from farmers in Namibia report that sheep are more skittish than goats and hence more likely to trigger predatory behaviour in LGDs (G. Potgieter pers. comm.).

In total, we monitored nine LGDs of Anatolian shepherd breed that were trained specifically to protect their designated livestock flocks 24 hours a day. Six of the LGDs (Farlas, Skollie, Kris, Ben, Lady and Toula) guarded their flocks independently without any human supervision, while three dogs (Rex, Fia and Lexi) were accompanied by an Ecoranger. Ecorangers were paid the minimum wage rate by the South African branch of the international NGO Conservation International ([www.conservation.org/south-africa](http://www.conservation.org/south-africa)), thanks to a grant from a major food retailer. They had various tasks in addition to accompanying and guarding livestock from predators. They corrected LGDs undesirable behaviour, collected ecological data (e.g. locations of scats and tracks of predators), monitored livestock health, soil erosion, the quality of the vegetation, and notified farmers of any problematic issues that they observed in the field. They worked from 8 a.m. to 5 p.m. seven days a week and remained in a semi-permanent camp in the field overnight, with work occurring in shifts to ensure constant human presence. All of the LGDs were sterilized and all except Kris, Lady and Toula originated from the same litter. To maximize the likelihood that dogs received similar training, each farmer was supplied with a management protocol by the NGO Cheetah Outreach (<http://www.cheetah.co.za/index.htm>),

which was then adapted and implemented by the SANParks Anatolian Shepherd Dog Breeding Project. Ecorangers were instructed to prevent LGDs from chasing wildlife, and this was also specified in their written training instructions. The dogs that were placed with Ecorangers were trained by those Ecorangers according to the same protocol. Site visits were conducted throughout the study by project partners to monitor the dogs and maintain consistency in their training.

LGDs were introduced to their flock at seven weeks of age, being placed in small enclosures (i.e. "kraals") for eight weeks with five ewes and five lambs or kids. At 16 weeks, the puppies and their small flocks of ten were moved to small camps to give them more freedom of movement. The puppies stayed with the sheep or goats for another eight weeks, accompanying them while they grazed. At 24 weeks, the small training flocks were reintegrated into the main flocks, and the dogs remained with their full flock permanently. The farmers and Ecorangers continued to train the dogs until they were one year old, correcting undesirable behaviours such as chasing livestock and wildlife and returning to the farmer's house. Automatic feeders were placed at livestock water points, giving the LGDs a reliable source of *ad-libitum* dog food. Dogs were observed by researchers, Ecorangers and farmers visiting both the water points and feeders. At the start of the dog diet study (when the dogs were just over one year old), all nine LGDs were equipped with GPS radio-collars.

### Scat collection and analyses

Scats from six LGDs (Farlas, Skollie, Kris, Ben, Rex, Fia) were collected in 2015-2016 in three ways: opportunistically when carrying out other field activities, at GPS clusters formed by GPS-collared LGDs, and directly by Ecorangers who were with some of the LGDs. Scat samples were placed in paper envelopes, labelled and dried at the field station at ambient temperature before being transported to the lab for processing. Scat samples were sterilised by autoclaving at 120 °C for 20 minutes. To separate food fragments from the matrix of the scat, each scat sample was placed in a nylon stocking tied at both ends and soaked in hot water overnight. In the morning, each stocking was opened and washed through a sieve (Klare et al. 2011). Once washed, remains (hairs, bones, vegetation, etc.) were spread out on a Petri dish and dried in an oven at 40 °C for 12 hours



before being weighed. The hairs were then soaked in 70% ethanol to remove any remaining faecal particles, rinsed with distilled water and allowed to dry under a fume hood for at least 24 hours prior to analysis. Macroscopic and microscopic identification were used to identify food items in each scat to the lowest possible taxonomic level. Undigested remains were separated into the following 15 broad categories: micromammals, small carnivores, rock hyrax (*Procapra capensis*), hares, Cape porcupine (*Hystrix africaeaustralis*), wild ungulates, domestic ungulates, unidentified mammals, invertebrates, birds, reptiles, fruit, vegetation, anthropogenic items and unknown (sensu Drouilly et al. 2018). The micromammal category included shrews and small rodents. Birds, reptiles, and invertebrates generally could not be identified any further, as the remains in scat samples were too fragmented to allow for accurate identification. Some scats only contained small bone fragments, which were identified by two small-mammal experts at the Iziko South African Museum, Cape Town. Mammalian remains were identified to species level through the microscopic analysis of hair cross-sections and longitudinal hair scale patterns (Klare et al. 2011). Unidentified items were recorded as unknown.

Mammal hair cross-sections were prepared using the method proposed by Douglas (1989). Twenty hairs were randomly selected with forceps and placed longitudinally into a 3-millimetre plastic Pasteur pipette (Douglas 1989, Spaulding et al. 2000). Molten, transparent wax (Surgipath Paraplast, Leica Microsystems, Wetzlar, Germany) was drawn into the pipette to provide a matrix for hair cross-sections (Douglas 1989). The pipette was then immediately placed in a beaker of ice to allow the wax to set (Keogh 1983, Douglas 1989). Once set, a razor-sharp surgical blade was used to slice five thin cross-sections from the plastic pipette. Cross-sections were mounted on a glass slide and examined under a Leica DM500 compound microscope at 40× magnification (Leica Microsystems, Wetzlar, Germany) (Douglas 1989, Drouilly et al. 2018). Imprints of hair cuticle patterns were used to verify initial identification and were prepared according to the method proposed by Dreyer (1966). A thin layer of clear nail polish was placed on a glass slide and allowed to dry for 20 seconds. Hairs were then randomly selected and placed on top of the slide. Hairs were then left to dry for at least one hour to allow the imprint to set before being carefully removed with

fine-tip tweezers. Hair imprints were examined under a Leica DM500 compound microscope at 40× magnification. Species were identified by comparing samples with reference keys (Dreyer 1966, Perrin & Campbell 1979, Keogh 1983, 1985, Brassine & Parker 2012).

Macroscopic remains such as bones and teeth were used to corroborate hair analysis (Drouilly et al. 2018). When hair was not present in a sample, identification was made by comparing bones and teeth to an established key (Avery 1979) and specimens held at the Iziko South African Museum. All food item identification was conducted blind, without knowledge of the assigned treatment (e.g. LGD working alone *vs.* accompanied by Ecoranger) to avoid potential bias (Martínez-Gutiérrez et al. 2015).

### Cluster investigation and analyses

Nine LGDs were collared with GPS radio-collars with UHF download capability (Africa Wildlife Tracking, Pretoria, South Africa) and monitored from April 2015 to March 2016. The fix rate was set to one location every three hours. We used a Python algorithm to identify clusters (Knopff et al. 2009), where the seed cluster included two locations within 50 m and six days of each other, and was thereafter allowed to expand within the same spatio-temporal constraints (Cristescu et al. 2015). Clustered locations where a collared LGD remained for more than three hours might indicate a feeding or a resting site (sensu Knopff et al. 2009, Cristescu et al. 2015). Once clusters were identified by the algorithm, we visited a random sample of them and systematically searched for food remains (i.e. carcasses, bone fragments, hairs, rumen, feathers) on a 50 m radius from the cluster centroid identified by the algorithm.

Total search time was standardized as two person-hours per site, with the exception of cluster sites where shrub cover was  $\leq 50\%$ , in which case total search time was reduced to one person-hour (Jansen et al. 2019). We started the search at the centroid of the cluster and walked outwards to the edge of the 50 m radius. Searching followed a zigzag pattern, initiated on a random direction and covered a quarter of an imaginary disk of the given radius. The centroid was then revisited and the search was iterated three additional times to cover the remaining quarters of the disk (Jansen et al. 2019). The species and where possible, sex and age of dead animals were determined. We estimated

the mean amount of time LGDs spent at clusters we visited based on the number of GPS locations at the cluster, after eliminating outliers (e.g. caused by LGDs returning periodically to the water point). Collars were manually removed from LGDs at the end of the experiment.

### Statistical analyses

The frequency of occurrence (FO) of each food item was calculated for both LGD scats and clusters. The frequency of occurrence was calculated as the number of times a food item was consumed, divided by the total number of food items identified from all scats/clusters. This number was expressed as a percentage for additional clarity (Klare et al. 2011). Whereas this calculation is one of the most common methods for reporting predator diet (Klare et al. 2011) and thus for comparing results between studies, it has been criticized for overestimating the importance of small food items (Weaver 1993, Klare et al. 2011). When carnivores feed on small items, they consume less food mass to excrete one scat than when they feed on larger items with more digestible meat and a lower surface to volume ratio (Floyd et al. 1978, Weaver 1993). Furthermore, unlike large items, multiple small food items (such

as insects) can occur in a single scat, which can further inflate their importance (Klare et al. 2011). To avoid such potential bias, a corrected frequency of occurrence (RFO) was also used in scat analysis to allow food items to be weighted accordingly (Floyd et al. 1978, Mann et al. 2019). To calculate this relative frequency of occurrence, each scat was given a total weighting of one. For example, if two food items were present, they each received a weighting of 0.5; whereas if four items were present, each was weighted as 0.25.

LGD scats and clusters were divided into two separate groups according to treatment types: 1) LGDs accompanied by an Ecoranger and 2) unsupervised LGDs. For each food item, its frequency of occurrence was compared among treatments using a Chi-squared test (or a Fisher's exact test when expected FO values were < 5%) to evaluate similarities and differences in diet by treatment type (Reynolds & Aebischer 1991, Drouilly et al. 2018). LGD diet specialization was calculated both from scats and clusters according to Levins' measure of niche breadth (Levins 1968, Krebs 1999):  $B = (1/\sum p_j^2)$  where  $p_j$  is the proportion of food items in the diet that are of

**Table 1.** Dietary composition of livestock guarding dogs (n = 6) derived from scat analyses, in Namaqualand, South Africa (2015-2016). Diet composition is expressed as frequency of occurrence (FO) and relative frequency of occurrence (RFO) per scat. A total of 183 scats were analysed, yielding 234 unique food occurrences.

Dietary items	Number of occurrences	FO (%)	Number of	RFO (%)
	(food items) n = 234		occurrences (per scat) n = 183	
Invertebrates	9	3.8	4.2	2.3
Birds	1	0.4	0.3	0.2
Reptiles	3	1.3	1.5	0.8
Mammals	150	64.1	134.8	73.7
Micromammals	8	3.4	5.8	3.2
Small carnivores	1	0.4	1.0	0.5
Hyrax	10	4.3	7.0	3.8
Hares	6	2.6	4.8	2.6
Porcupine	4	1.7	4.0	2.2
Wild ungulates	11	4.7	8.8	4.8
Domestic ungulates	108	46.2	101.8	55.6
Unidentified mammals	2	0.9	1.5	0.8
Fruit	2	0.9	0.7	0.4
Vegetation	49	20.9	32.2	17.6
Anthropogenic items	11	4.7	4.7	2.6
No prey items*	1	0.4	1.0	0.5
Unidentified	8	3.4	3.5	1.9

\* One scat sample contained only gravel.



category  $j$ . We standardized the measure of niche breadth (Hurlbert 1978) to account for sample size differences between dogs and to express it on a scale from 0 to 1 as:  $B_s = (B - 1)/(n - 1)$  where  $n$  is the number of possible resource states (seven general categories in the case of scats and eight in the case of clusters). We also determined dietary niche overlap among accompanied LGDs and non-accompanied LGDs by applying Pianka's index (Pianka 1973) to the scat analysis data (using the same seven broad categories as in the calculation of niche breadth). This measure ranges from 0 (no prey in common) to 1 (complete overlap in diet). We transformed the values into percentage overlap by calculating the Renkonen index ( $R$ ; Krebs 1999).

## Results

### Scat analysis

The 183 scats mostly contained mammals (73.7%) representing 12 different species (i.e. only 15.8% of scats did not include mammals). The RFO of mammals in LGD scats varied from 9.1% for Fia (accompanied by an Ecoranger) to 95.5% for Farlas (unaccompanied). The majority of the scats (76%)

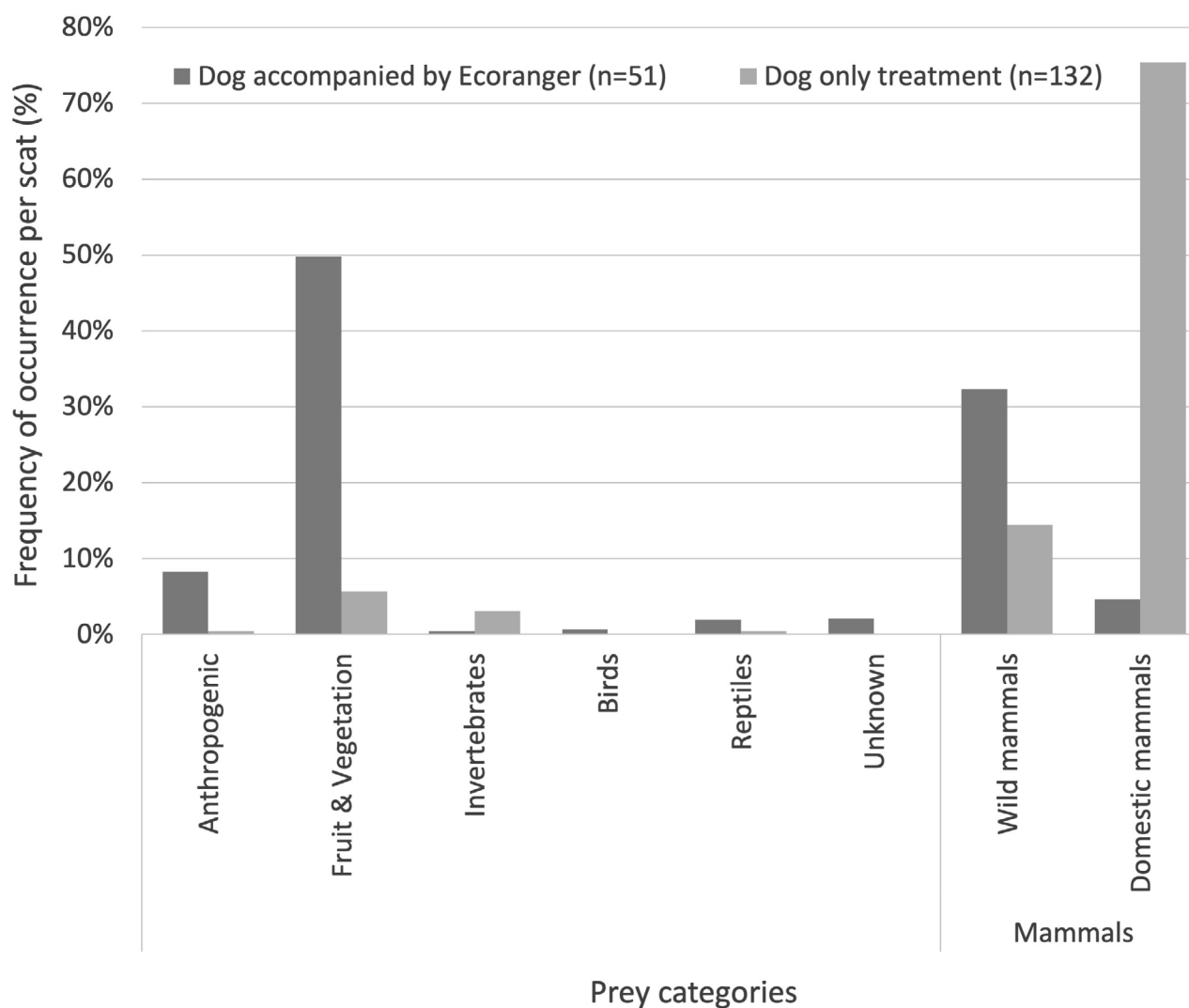
comprised a single food item, with 21% having two food items, only 2% having three and a single sample having five different food items. Only one scat did not contain any evidence of plant or wildlife species.

Animal remains were dominated by domestic ungulates, which occurred in 60% of scat samples and had relative frequency of occurrence (RFO) of 55.6% (Table 1). The RFO per scat of goats was 3.8% and 51.8% for sheep. The next most common mammalian prey category was wild ungulates, which occurred in 6% of scats and had an RFO of 4.8% (Table 1). Wild mammalian prey items were quite diverse, with ten different species identified (in order of most to least frequent): rock hyrax, scrub hare (*Lepus saxatilis*), Cape porcupine, klipspringer (*Oreotragus oreotragus*), common duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), bush vlei rat (*Otomys unisulcatus*), meerkat (*Suricata suricatta*), Namaqua rock mouse (*Micaelamys namaquensis*), and springbok (*Antidorcas marsupialis*). Birds and reptiles occurred in less than one percent of scats, whereas invertebrates were slightly more common (2.3%) (Table 1). Beetles were the most frequently detected invertebrate.

**Table 2.** Dietary composition of livestock guarding dogs ( $n = 9$ ) following GPS cluster investigation, in Namaqualand, South Africa (2015-2016). Diet composition is expressed as frequency of occurrence (FO). A total of 352 clusters were visited, yielding 116 unique food occurrences.

Food items found at GPS clusters	All LGDs		LGDs with Ecoranger		Unaccompanied LGDs	
	Number of food items $n = 116$	FO (%)	Number of food items $n = 16$	FO (%)	Number of food items $n = 100$	FO (%)
Birds	4	3.4	1	6.2	3	3
Raptor	2	1.7	1	6.2	1	1
Other bird species	2	1.7	0	0	2	2
Mammals	111	95.7	13	81.3	95	95
Hyaxes	8	6.9	3	18.8	5	5
Hares	7	6.0	2	12.5	5	5
Wild ungulates	8	6.9	2	12.5	6	6
Common duiker	2	1.7	1	6.2	1	1
Steenbok	3	2.6	1	6.2	2	2
Springbok	3	2.6	0	0	3	3
Domestic ungulates	79	68.1	5	31.3	74	74
Goat	6	5.2	3	18.8	3	3
Sheep	73	62.9	2	12.5	71	71
Unidentified mammals	9	7.8	1	6.2	5	5
Unidentified food item	1	0.9	2	12.2	2	2





**Fig. 2.** Differences in diet composition of livestock guarding dogs across two selective predator management types: dogs guarding their flocks alongside human attendants known as Ecorangers; and dogs operating independently.

### GPS clusters

The length of time GPS collars were on the dogs and collecting data ranged from 102 days (607 locations) to 353 days (2326 locations) (mean  $\pm$  SD = 250.8 days  $\pm$  112.9; mean  $\pm$  SD = 1552.2  $\pm$  718.4 locations). The mean time from cluster formation to investigation was 57  $\pm$  32 days (range: 3-161 days), therefore successfully differentiating between predation and scavenging was rare. Collars recorded on average 3  $\pm$  2 locations at a cluster, corresponding to 6  $\pm$  3 hours (range: 1-9 locations corresponding to 3-27 hours). A total of 352 clusters were visited for the nine LGDs collared. Carcasses were found at 33.2% of all clusters investigated (i.e. 66.8% of the clusters had no carcass associated with them), and varied from 0% for Fia (accompanied by an Ecoranger) to 53.5% for Skollie (unaccompanied).

### Diet of LGDs with Ecorangers vs. unaccompanied

The diet of dogs accompanied by Ecorangers was significantly different from the diet of

unaccompanied dogs ( $\chi^2 = 94.08$ ,  $p < 0.001$ ). There was no significant difference in proportion of the diet comprising mammals ( $\chi^2 = 1.07$ ,  $p = 0.302$ ) between accompanied (FO: 81.3%) vs. independent LGDs (FO: 95%) (Table 2). Although more of the scats of LGDs with Ecorangers contained wild mammals (FO: 32.3%, range = 5.1-59.8%) compared to the scats of unaccompanied dogs (FO: 14.4%, range = 12.2-25.0%), though the difference was not significant ( $\chi^2 = 0.18$ ,  $p = 0.675$ ). There was also no significant difference ( $\chi^2 = 2.28$ ,  $p = 0.131$ ) in the consumption of wild ungulates between the two treatments; but both hares and hyraxes were found significantly more often in the clusters of accompanied compared to unaccompanied dogs (Table 2).

Domestic ungulate remains occurred in less than 5% (n = 2) of scats for LGDs with an Ecoranger (range = 0-6.1%), compared to more than 75% of scats retrieved from unaccompanied LGDs



(range = 25.0-82.8%) (Fig. 2). Of the two scats containing livestock for LGDs accompanied by an Ecoranger, one sample comprised goat hair and bones and the other included only a few sheep hairs, lacking a definitive indication of livestock consumption (e.g. bones or pieces of skin). Similar results were obtained from cluster analyses, with significantly lower ( $\chi^2 = 17.31, p < 0.001$ ) occurrence of domestic ungulates at clusters of LGDs with Ecorangers (FO: 31.3%, range = 0-44.4%) compared to unaccompanied dog clusters (FO: 74%, range = 20-91.9%). This difference was largely attributed to lower proportion ( $\chi^2 = 40.98, p < 0.001$ ) of sheep remains at clusters of LGDs with Ecorangers (FO: 12.5%), compared to unaccompanied dogs' clusters (FO: 71%).

For LGDs accompanied by Ecorangers, 43.8% of the clusters with carcasses ( $n = 16$ ) contained wild mammals (range = 0.0-71.4%), whereas for LGDs guarding on their own, only 16% of clusters with carcasses ( $n = 100$ ) had wild mammal remains (range = 4.3-60.0%). The scats of dogs accompanied by Ecorangers contained significantly more plants than the scats of their unaccompanied counterparts ( $\chi^2 = 9.74, p = 0.002$ ; Fig. 2), as well as more anthropogenic material (Fig. 2).

### LGDs diet specialization and dietary niche overlap amongst treatments

The standardized measure of niche breadth was much higher for LGDs with Ecorangers (0.20 through scat analysis and 0.92 through cluster analysis) than for their solitary counterparts (0.08 through scat analysis and 0.11 through cluster analysis). Thus, while unaccompanied LGDs focussed more on consuming sheep, LGDs with Ecorangers had a more generalist diet. Using the results from scat analysis and the Pianka's index, we found that dietary niche overlap between accompanied and non-accompanied LGDs was 0.238, which corresponds to 25.9% overlap.

## Discussion

This study marks the first attempt, to our knowledge, to quantify the diet composition of LGDs working on farmland. As expected, we found both wildlife and livestock in the diet of LGDs, but their RFO differed according to whether or not the dogs were accompanied by an Ecoranger. As predicted, LGDs with Ecorangers consumed less livestock than those unaccompanied, but contrary to our prediction, they ate more wildlife.

Neither of our diet assessment methods could unequivocally discern between predated versus scavenged prey and this remains a challenge for future studies. Scavenging behaviour has been observed in LGDs on African farmland (van Vliet 2011, Whitehouse-Tedd et al. 2020) and has been argued to have inflated estimates of livestock killed in other diet studies (Chavez & Gese 2005). However, it is well established that some LGDs chase and kill both wildlife and domestic animals on farmland (Green et al. 1984, Timm & Schmidtz 1989, Smith et al. 2000, Hansen et al. 2002, Marker et al. 2005a, b, Gingold et al. 2009, Potgieter et al. 2013, 2016). One study surveyed 45 owners of 137 LGDs (Anatolian shepherd dogs were one of five breeds included in the study) cooperating in a study at the U.S. Sheep Experiment Station (Green et al. 1984). Fourteen of the dogs had injured or killed livestock in their lifetime and five of those dogs became habitual livestock killers. Seven farmers owned fully-grown dogs that continued to "play" after maturation and chased sheep until they eventually killed them and had to be put down (Green et al. 1984). In Namibia, chasing wildlife is one of the most commonly reported behavioural problems in LGDs (Marker et al. 2005a, b, Potgieter et al. 2013). Dogs have been reported to chase and consume wildlife as large as kudu (*Tragelaphus strepsiceros*; mean adult female body mass: 180 kg (du Toit 1990)) (Potgieter et al. 2016). There have also been some reports suggesting that LGDs will kill and consume small rodents and young fawns (Timm & Schmidtz 1989, Urbigkit 2017) and that small-mammal populations may be negatively impacted in pasture with LGDs (VerCauteren et al. 2014 in Whitehouse-Tedd et al. 2020). Suspecting that malnourishment could either encourage LGDs to hunt or rob them of the energy to chase wildlife, Potgieter et al. (2013) investigated whether the level of care provided influenced a dog's propensity to chase wildlife. Commercial farmers (such as the ones in the present study) were found to provide significantly better care to their LGDs than subsistence farmers (Potgieter et al. 2013). However, level of care was not found to differ between LGDs that chased wildlife and those that did not (Potgieter et al. 2013). Although domestic dogs more generally have been shown to increase predation when poorly fed (Silva-Rodríguez & Sieving 2011), it is unlikely to be a contributing factor in this study as the LGDs had constant access to a trough of pelleted dog food. Thus, LGDs in our study did not need to supplement an inadequate diet with hunting.



Our small sample size precluded us from investigating whether livestock type had an influence on LGDs predatory/feeding behaviour. Goats might be more accepting of the presence of LGDs than sheep but they were also less abundant, which might explain why we found more sheep remains than goats in the scats of LGDs. Similarly, LGD sex and age, as well as the training and experience of farmers and Ecorangers are likely to have an influence on the success of the method. Future studies should investigate these variables as well as the influence of livestock type (species and breed) and livestock behaviour on the propensity of LGDs to chase and kill livestock.

None of the scat samples or GPS clusters contained potential livestock predators such as caracal or black-backed jackal and Ecorangers infrequently witnessed LGDs chasing mesopredators. A study of 79 LGDs placed on Namibian farms revealed 56% of the dogs killed predator species (Potgieter et al. 2016). Black-backed jackals were killed by 37 dogs, baboons (*Papio* sp.) were killed by eight dogs, caracals were killed by three dogs, and one dog killed a cheetah (*Acinonyx jubatus*) that jumped into a livestock enclosure during the night (Potgieter et al. 2016). The deaths of a bat-eared fox (*Otocyon megalotis*) and African wildcats (*Felis sylvestris*) were also reported (Potgieter et al. 2016). Killing of wildlife by LGDs aligns with the hypothesis of Allen et al. (2019) that LGDs may act as human-introduced predators on rangeland. It is possible that the Anatolian shepherd dogs in this study also killed predators that threatened the flocks but did not consume their remains, in which case these incidents would have gone undetected by our methods. Direct observation or remote video footage from either camera traps or collar-mounted cameras could be used to determine the percentage of food items coming from scavenging *vs.* predation behaviour. Another, expensive but more accurate method would be to use collars with tri-axial accelerometers (Wang et al. 2015) and fine-scale GPS recordings (Fehlman et al. 2017) to determine when, where and how often LGDs are hunting *vs.* scavenging (and what species they are hunting after investigation of GPS clusters in the field). These approaches could also illuminate whether LGDs kill more wildlife than they consume, which has been reported in Namibia (Marker et al. 2005b, Potgieter et al. 2016), and in studies on free-ranging dogs (Taborsky 1988). On

the contrary, we cannot eliminate the possibility that in some cases LGDs found existing carcass that died of other causes (e.g. wild predator, poisonous plant, disease) without consuming it, though still forming a cluster of GPS points at the site. Consumption was difficult to differentiate due to the relatively long interval between cluster formation and investigation. However, there was some consistency between findings from cluster visits and scat analysis, suggesting that at least some clusters represented carcass consumption by the LGDs. Nonetheless, we recommend that future studies decrease the time elapsed between cluster formation and investigation as this will allow differentiation of consumption and even predation versus scavenging.

Individual traits and personalities can have a strong impact on working dog behaviour (Helton 2009) and may play a role in the proclivity of LGDs to harass other animals. This possibility was evident from this study with marked differences between dogs from the same litter, raised and trained within the same program at the same time and supplied with the same type and amount of pelleted dog food. For example, Fia consumed by far the most vegetation and anthropogenic food and was the only dog that did not have any livestock remains in her scats, while Rex consumed mostly wild ungulates and some livestock, despite both dogs being accompanied by an Ecoranger. Thus, caution is needed when generalizing the ecological impact of LGDs (as was the case in Allen et al. 2019) as they have been shown to be environmentally and temporally context-dependent (Ritchie et al. 2014). Corrective training of unwanted behaviours in LGDs by shepherds has proven successful in many cases (Green et al. 1984, Hansen et al. 2002, Marker et al. 2005a, b). In Namibia, wildlife chasing appears to be declining in the overall population of LGDs and trustworthiness has increased thanks to improvements in training methods (Potgieter et al. 2013). A study on reported LGD-wildlife interactions in South Africa also showed that, of the LGDs for which data on corrective measures were available, 44% were successfully corrected following behavioural interventions by the project managers or farmers. Of those considered not corrected, 42% had stopped exhibiting this behaviour independently or were considered to be acting defensively when confronted by a potential threat to the livestock (Whitehouse-Tedd et al. 2020).



Swift action is clearly crucial to the success of corrective training in LGDs. However, in order for the correction to take place, the dogs must have regular human supervision (Marker et al. 2005b). In this study, LGDs paired with Ecorangers had a low occurrence of livestock in their scat and at location clusters. This finding suggests that the presence of an Ecoranger either directly limits the consumption of livestock by the LGD, or allows for the immediate corrective behaviour when it is witnessed so it does not become habitual. Ecorangers stopped the LGDs if they tried to chase livestock, a behaviour that was more prevalent when the LGDs were young. Domestic dogs more broadly have been known to avoid preying when humans are near (Ciucci & Boitani 1998). In central Italy, for example, out of 50 attacks by free-ranging dogs on livestock, not one occurred while a shepherd was in proximity (Ciucci & Boitani 1998). Human presence also mimics the way LGDs developed historically. Originally, they guarded small flocks accompanied by a human herder; a different scenario from the large flocks they often guard independently today (Smith et al. 2000).

Researchers in Norway are resurrecting this approach by promoting a combination of herding and guarding (Hansen et al. 2002). Although dogs in the study of Hansen et al. (2002) were also reported to chase livestock and wildlife, this behaviour was swiftly and successfully corrected by their attendant. Importantly, this approach was also associated with a significant reduction in predation, but only in small (10–12 km<sup>2</sup>) pastures (Hansen et al. 2002). This approach is potentially of great value to South African small-livestock as it was developed for sheep that do not flock, typical of sheep breeds on semi-arid extensive farmland. An important consideration is that any training and management to prevent the consumption of livestock should also be applied to wildlife. In our study and contrary to our prediction, LGDs accompanied by an Ecoranger consumed more wildlife than their solitary counterparts, a result supported by evidence from both scat and GPS cluster analyses. Accompanied LGDs also had a broader dietary niche breadth than unaccompanied LGDs. Interestingly, LGDs only had a 25.9% dietary overlap between treatments, showing the importance of the presence of Ecorangers on LGD diets.

While human vigilance and corrective behaviour are clearly beneficial in reducing the consumption

of domestic ungulates by LGDs, they come with a substantial price tag (Saitone & Bruno 2020). Labour costs for shepherds are prohibitive for many small farms in arid areas with restricted budgets, limited infrastructure and extensive grazing areas (Hansen et al. 2002, Nattrass & Conradie 2015). However, Ecorangers were not paid at a higher wage than normal farm labourers (i.e. minimum wage). As demonstrated in other studies, some financial support from the local or national government or consumer-based support to employ Ecorangers (to guard sheep and conduct other conservation tasks) is urgently needed in the current context of the environmental and socio-economic crisis facing small-livestock farming in southern Africa (Drouilly et al. 2018, Nattrass & Conradie 2018, Nattrass et al. 2019). We were unable to provide information on how many livestock LGDs killed, which farmers would need to know to reliably inform their management decisions. Further studies on that topic would be valuable to farmers and farm productivity.

LGDs have been shown in many studies to be an effective tool for livestock protection and carnivore conservation (Green et al. 1984, Andelt 1992, Andelt & Hopper 2000, Smith et al. 2000, Hansen et al. 2002, Marker et al. 2005a, b, Potgieter et al. 2013, 2016, Whitehouse-Tedd et al. 2020). This study does not cast doubt upon those findings. Rather, it seeks to illuminate the knowledge gaps in the ability and inclination of some LGDs to act as introduced predators on both wild and domestic species in their environment. Although the results of this study should be regarded as preliminary due to the small sample sizes, there is evidence that human presence can reduce the consumption of livestock. While too much human contact could reduce their effectiveness at livestock guarding, human presence should be regular enough to take swift corrective action for any undesirable behaviour (Marker et al. 2005b).

## Conclusions

This study reveals that while LGDs are a widespread form of responsible, selective predator management in southern Africa and globally, they can pose a risk to both wildlife and livestock. The most frequently consumed animal food item of LGDs in this study was livestock. Although sample sizes were small, the near absence of livestock from the scats of dogs accompanied by Ecorangers suggests that human presence may greatly reduce

this undesirable behaviour. However, it is important to note that human presence did not deter the dogs from consuming wild prey. Placement of LGDs should be accompanied by long-term monitoring (particularly in areas with threatened species), to record any negative effects on wild and domestic species that share their landscape. When chasing and killing other animals can be reduced through human presence and corrective training, the ability of LGDs to serve as both a primary and secondary repellent (Gehring et al. 2010) provides obvious benefits to farmer productivity (Green et al. 1984, Andelt 1992, Andelt & Hopper 2000, Smith et al. 2000, Marker et al. 2005b). The use of Ecorangers is an additional cost to farmers and is thus unlikely to be adopted unless the benefits to farm productivity outweigh these costs. Given the current poor socio-economic conditions facing small-livestock in semi-arid regions of South Africa, financial support (e.g. from local governments, consumers, etc.) to employ Ecorangers is necessary. Ecorangers in combination with LGDs offer an opportunity to foster human-carnivore coexistence (Rust et al. 2013) with reduced impacts on non-target species in addition to improved management of the land in which livestock live. When LGDs are combined with nonlethal methods and/or selective humane lethal methods, the options to move away from indiscriminate lethal management will improve and positive outcomes for farmers, livestock, and biodiversity may well be realized.

## Acknowledgements

We thank SANParks (Namaqua National Park), the Anatolian Dog Breeding Project, and private landowners for supporting the research and for allowing us to work in the area. We thank Woolworths Holdings Limited, Conservation South Africa, The Cape Leopard Trust, and additional sponsors (ABAX Foundation, Afrihost, Bridgestone, K-Way, Mica, Supa Quick, Ultra Dog) for providing funding and support. Karoo PEACE (Predator Ecology and Coexistence Experiment) team volunteers assisted with data collection and processing. We are grateful to Dr G. Avery and Dr M. Avery of the Iziko South African Museum for their expertise and aid in identifying bone fragments of prey items. We thank Dr D. Parker for providing the mammalian hair reference collection held at Rhodes University, South Africa. Finally, we thank G. Potgieter and an anonymous reviewer, as well as the journal editors for their comments that helped improve our manuscript. B. Cristescu was supported by a Claude Leon Foundation Postdoctoral Fellowship at the University of Cape Town and K.J. Teichman was supported by the Natural Sciences and Engineering Research Council Canada Graduate Scholarship – Doctoral at the University of British Columbia. Author contributions: M. Drouilly performed the analyses and led the writing of the manuscript, C. Kelly carried out laboratory work and performed the analyses, B. Cristescu and K.J. Teichman conceived the ideas and provided data, M.J. O’Riain supervised the study. All authors contributed critically to drafts and gave final approval for publication.



## Literature

- Allen B.L., Allen L.R., Ballard G. et al. 2019: Animal welfare considerations for using large carnivores and guardian dogs as vertebrate biocontrol tools against other animals. *Biol. Conserv.* 232: 258–270.
- Allen L.R., Stewart-Moore N., Byrne D. & Allen B.L. 2017: Guardian dogs protect sheep by guarding sheep, not by establishing territories and excluding predators. *Anim. Prod. Sci.* 57: 1118. <https://doi.org/10.1071/AN16030>.
- Andelt W.F. 1992: Effectiveness of livestock guarding dogs for reducing predation on domestic sheep. *Wildl. Soc. Bull.* 20: 55–62.
- Andelt W.F. & Hopper S.N. 2000: Livestock guard dogs reduce predation on domestic sheep in Colorado. *J. Range Manag.* 53: 259–267.
- Arthur L.M. 1981: Coyote control: the public response. *J. Range Manag.* 34: 14–15.
- Avery D.M. 1979: Upper Pleistocene and Holocene palaeoenvironments in the southern Cape: the micromammalian evidence from archaeological sites. *PhD thesis, University of Stellenbosch, South Africa.*
- Berger K.M. 2006: Carnivore-livestock conflicts: effects of subsidized predator control and economic correlates on the sheep industry. *Conserv. Biol.* 20: 751–761.
- Brassine M.C. & Parker D.M. 2012: Does the presence of large predators affect the diet of a mesopredator? *Afr. J. Ecol.* 50: 243–246.
- Casey A.L., Krausman P.R., Shaw W.W. & Shaw H.G. 2005: Knowledge of and attitudes toward mountain lions: a public survey of residents adjacent to saguaro national park, arizona. *Hum. Dimens Wildl.* 10: 29–38.
- Chavez A.S. & Gese E.M. 2005: Food habits of wolves in relation to livestock depredations in Northwestern Minnesota. *Am. Midl. Nat.* 154: 253–263.
- Ciucci P. & Boitani L. 1998: Wolf and dog depredation on livestock in central Italy. *Wildl. Soc. Bull.* 26: 504–514.
- Conradie B. & Nattrass N. 2017: The robustness of self-report data on predation: a comparison of two Karoo surveys. *African J. Agric. Resour. Econ.* 12: 217–229.
- Cowling R., Rundel P., Desmet P. & Esler K. 1998: Extraordinary high regional-scale plant diversity in Southern African arid lands: subcontinental and global comparisons. *Divers. Distrib.* 4: 27–36.
- Cristescu B., Stenhouse G.B. & Boyce M.S. 2015: Predicting multiple behaviors from GPS radiocollar cluster data. *Behav. Ecol.* 26: 452–464.
- Douglas R.M. 1989: A new method of cross-sectioning hair of larger mammals. *S. Afr. J. Wildl. Res.* 19: 73–76.
- Dreyer J.H. 1966: A study of hair morphology in the family bovidae. *Onderstepoort J. Vet. Res.* 33: 379–472.
- Driver A., Desmet P., Rouget M. et al. 2003: Succulent Karoo ecosystem plant biodiversity component technical report. *Cape Conservation Unit, Botanical Society of South Africa, Cape Town, South Africa.*
- Drouilly M., Nattrass N. & O'Riain M.J. 2018: Dietary niche relationships among predators on farmland and a protected area. *J. Wildl. Manag.* 82: 507–518.
- Drouilly M., Tafani M., Nattrass N. & O'Riain M.J. 2018: Spatial, temporal and attitudinal dimensions of conflict between predators and small-livestock farmers in the Central Karoo. *Afr. J. Range Forage Sci.* 35 (3–4): 245–255.
- du Toit J.T. 1990: Home range – body mass relations: a field study on African browsing ruminants. *Oecologia* 85: 301–303.
- Eklund A., López-Bao J.V., Tourani M. et al. 2017: Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. *Sci. Rep.* 7: 2097. <https://doi.org/10.1038/s41598-017-02323-w>.
- Fehlman G., O'Riain M.J., Hopkins P.W. et al. 2017: Identification of behaviours from accelerometer data in a wild social primate. *Anim. Biotelemetry* 5: 6. <https://doi.org/10.1186/s40317-017-0121-3>.
- Feldmann B.M. 1974: The problem of urban dogs. *Science* 185: 903–903.
- Floyd T.J., Mech L.D. & Jordan P.A. 1978: Relating wolf scat content to prey consumed. *J. Wildl. Manag.* 42: 528–532.
- Gehring T.M., Vercauteren K.C. & Landry 2010: Livestock protection dogs in the 21<sup>st</sup> century: is an ancient tool relevant to modern conservation challenges? *BioScience* 60: 299–308.
- Gingold G., Yom-Tov Y., Kronfeld-Schor N. & Geffen E. 2009: Effect of guard dogs on the behavior and reproduction of gazelles in cattle enclosures on the Golan Heights. *Anim. Conserv.* 12: 155–162.
- Green J.S., Woodruff R.A. & Tueller T.T. 1984: Livestock-guarding dogs for predator

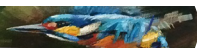


- control: costs, benefits, and practicality. *Wildl. Soc. Bull.* 12: 44–50.
- Hansen I., Staaland T. & Ringsø A. 2002: Patrolling with livestock guard dogs: a potential method to reduce predation on sheep. *Acta Agric. Scand. A* 52: 43–48.
- Helton W.S. 2009: Canine ergonomics – the science of working dogs. *Taylor & Francis Group, Boca Raton, Florida*.
- Hurlbert S.H. 1978: The measurement of niche overlap and some relatives. *Ecology* 59: 67–77.
- Jansen C., Leslie A.J., Cristescu B. et al. 2019: Determining the diet of an African mesocarnivore, the caracal: scat or GPS cluster analysis? *Wildl. Biol.* 2019: wlb.00579. <https://doi.org/10.2981/wlb.00579>.
- Keogh H.J. 1983: A photographic reference system of the microstructure of the hair of southern African bovids. *S. Afr. J. Wildl. Res.* 13: 89–131.
- Keogh H.J. 1985: A photographic reference system based on the cuticular scale patterns and groove of the hair of 44 species of southern African Cricetidae and Muridae. *S. Afr. J. Wildl. Res.* 15: 109–159.
- Klare U., Kamler J.F. & MacDonald D.W. 2011: A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Rev.* 41: 294–312.
- Knopff K.H., Knopff A.A., Warren M.B. & Boyce M.S. 2009: Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. *J. Wildl. Manag.* 73: 586–597.
- Krebs C.J. 1999: Ecological methodology, 2<sup>nd</sup> ed. *Addison-Wesley Educational Publishers, Inc., Menlo Park, California*.
- Leijenaar S.-L., Cilliers D. & Whitehouse-Tedd K. 2015: Reduction in livestock losses following placement of livestock guarding dogs and the impact of herd species and dog sex. *J. Agric. Biodivers. Res.* 4: 9–15.
- Levins R. 1968: Evolution in changing environments: some theoretical explorations. *Princeton University Press, Princeton, New Jersey*.
- Lindzey F. & Wilbur C. 1989: Estimating domestic sheep losses to mountain lions. *Great Plains Wildlife Damage Control Workshop Proceedings, University of Nebraska, Lincoln*: 27–31.
- Linnell J.D.C., Odden J. & Mertens A. 2012: Mitigation methods for conflicts associated with carnivore depredation on livestock. In: Boitani L. & Powell R. (eds.), *Carnivore ecology and conservation*. *Oxford University Press, Oxford*: 314–332.
- Mann G.K.H., Wilkinson A., Hayward J. et al. 2019: The effects of aridity on land use, biodiversity and dietary breadth in leopards. *Mamm. Biol.* 98: 43–51.
- Marker L., Dickman A. & Schumann M. 2005a: Using livestock guarding dogs as a conflict resolution strategy on Namibian farms. *Carniv. Damage Prev. News* 8: 28–32.
- Marker L.L., Dickman A.J. & Macdonald D.W. 2005b: Perceived effectiveness of livestock-guarding dogs placed on Namibian farms. *Rangeland Ecol. Manag.* 58: 329–336.
- Martínez-Gutiérrez P.G., Palomares F. & Fernández N. 2015: Predator identification methods in diet studies: uncertain assignment produces biased results? *Ecography* 38: 922–929.
- Minnie L., Gaylard A. & Kerley G.I.H. 2016: Compensatory life-history responses of a mesopredator may undermine carnivore management efforts. *J. Appl. Ecol.* 53: 379–387.
- Natrass N. & Conradie B. 2015: Jackal narratives: predator control and contested ecologies in the Karoo, South Africa. *J. South. Afr. Stud.* 41: 753–771.
- Natrass N. & Conradie B. 2018: Predators, livestock losses and poison in the South African Karoo. *J. Clean. Prod.* 194: 777–785.
- Natrass N., Conradie B., Stephens J. & Drouilly M. 2019: Culling recolonizing mesopredators increases livestock losses: evidence from the South African Karoo. *Ambio* 49: 1222–1231.
- Naughton-Treves L. & Treves A. 2005: Evaluating lethal control in the management of human-wildlife conflict. In: Woodroffe R., Thirgood S. & Rabinowitz A. (eds.), *People and wildlife: conflict or coexistence?* *Cambridge University Press, New York, USA*: 86–106.
- Perrin M.R. & Campbell B.S. 1979: Key to the mammals of the Andries Vosloo Kudu Reserve (eastern Cape), based on their hair morphology, for use in predator scat analysis. *S. Afr. J. Wildl. Res.* 10: 1–14.
- Pianka E.R. 1973: The structure of lizard communities. *Annu. Rev. Ecol. Syst.* 4: 53–74.
- Potgieter G.C., Kerley G.I.H. & Marker L.L. 2016: More bark than bite? The role of livestock guarding dogs in predator control on Namibian farmlands. *Oryx* 50: 514–522.
- Potgieter G.C., Marker L.L., Avenant N.L. & Kerley G.I.H. 2013: Why Namibian farmers are satisfied with the performance of their livestock guarding dogs. *Hum. Dimens Wildl.* 18: 403–415.
- Reiter D.K., Brunson M.W. & Schmidt R.H. 1999: Public attitudes toward wildlife damage



- management and policy. *Wildl. Soc. Bull.* 27: 746–758.
- Reynolds J.C. & Aebischer N.J. 1991: Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. *Mammal Rev.* 21: 97–122.
- Ritchie E., Dickman C., Letnic M. & Vanak A. 2014: Dogs as predators and trophic regulators. In: Gompper M.E. (ed.), *Free-ranging dogs and wildlife conservation*. Oxford University Press, Oxford, UK: 55–68.
- Rochlitz I., Pearce G. & Broom D. 2010: The impact of snares on animal welfare. *University of Cambridge Press, Cambridge, UK*.
- Rust N.A., Whitehouse-Tedd K.M. & MacMillan D.C. 2013: Perceived efficacy of livestock-guarding dogs in South Africa: implications for cheetah conservation. *Wildl. Soc. Bull.* 37: 690–697.
- Saitone T.L. & Bruno E.M. 2020: Cost effectiveness of livestock guardian dogs for predator control. *Wildl. Soc. Bull.* doi: <https://doi.org/10.1002/wsb.1063>.
- Silva-Rodríguez E.A. & Sieving K.E. 2011: Influence of care of domestic carnivores on their predation on vertebrates. *Conserv. Biol.* 25: 808–815.
- Slagle K., Bruskotter J.T., Singh A.S. & Schmidt R.H. 2017: Attitudes toward predator control in the United States: 1995 and 2014. *J. Mammal.* 98: 7–16.
- Smith M.E., Linnell J.D.C., Odden J. & Swenson J.E. 2000: Review of methods to reduce livestock depredation: I. Guardian animals. *Acta Agric. Scand. A* 50: 279–290.
- Spaulding R., Krausman P.R. & Ballard W.B. 2000: Observer bias and analysis of gray wolf diets from scats. *Wildl. Soc. Bull.* 28: 947–950.
- Spencer K., Sambrook M., Bremner-Harrison S. et al. 2020: Livestock guarding dogs enable human-carnivore coexistence: first evidence of equivalent carnivore occupancy on guarded and unguarded farms. *Biol. Conserv.* 241: 108256. <https://doi.org/10.1016/j.biocon.2019.108256>.
- Stannard C. & Cilliers D. 2018: Livestock guarding dog project progress report. *Cheetah Outreach Trust, South Africa*.
- Stoddart L.C., Griffiths R.E. & Knowlton F.F. 2001: Coyote responses to changing jackrabbit abundance affect sheep predation. *J. Range Manag.* 54: 15–20.
- Taborsky M. 1988: Kiwis and dog predation: observations at Waitangi State Forest. *Notornis* 35: 197–202.
- Teichman K.J., Cristescu B. & Darimont C.T. 2016: Hunting as a management tool? Cougar-human conflict is positively related to trophy hunting. *BMC Ecol.* 16: 44. <https://doi.org/10.1186/s12898-016-0098-4>.
- Thorn M., Green M., Dalerum F. et al. 2012: What drives human-carnivore conflict in the North West Province of South Africa? *Biol. Conserv.* 150: 23–32.
- Timm R. & Schmidt R. 1989: Management problems encountered with livestock guarding dogs on the University of California, Hopland Field Station. *Great Plains Wildlife Damage Control Workshop Proceedings, University of Nebraska, Lincoln*: 54–58.
- Torres D.F., Oliveira E.S. & Alves R.R.N. 2018: Conflicts between humans and terrestrial vertebrates: a global review. *Trop. Conserv. Sci.* 11: 1–15.
- Treves A., Krofel M. & McManus J. 2016: Predator control should not be a shot in the dark. *Front. Ecol. Environ.* 14: 380–388.
- Urbigkit C. 2017: Brave and loyal: an illustrated celebration of livestock guardian dogs. *Skyhorse Publishing, New York, USA*.
- Urbigkit C. & Urbigkit J. 2010: A review: the use of livestock protection dogs in association with large carnivores in the Rocky Mountains. *Sheep Goat Res. J.* 25: 1–8.
- van Bommel L. & Johnson C. 2017: Predation control. In: Ferguson D., Lee C. & Fisher A. (eds.), *Advances in sheep welfare*. Woodhead Publishing, Duxford, UK: 177–196.
- van Eeden L.M., Crowther M.S., Dickman C.R. et al. 2018: Managing conflict between large carnivores and livestock. *Conserv. Biol.* 32: 26–34.
- van Niekerk H.N. 2010: The cost of predation on small livestock in South Africa by medium-sized predators. *MSc thesis, University of the Free State, Bloemfontein, South Africa*.
- van Vliet C. 2011: Livestock guarding dogs do not hunt on secondary food sources – using scat analysis. *MSc thesis, Wageningen University, The Netherlands*.
- VerCauteren K.C., Lavelle M.J., Gehring T.M. et al. 2014: Dogs as mediators of conservation conflicts. In: Gompper M.E. (ed.), *Free-ranging dogs and wildlife conservation*. Oxford University Press, Oxford, UK: 211–233.





- Wang Y., Nickel B., Rutishauser M. et al. 2015: Movement, resting, and attack behaviors of wild pumas are revealed by tri-axial accelerometer measurements. *Mov. Ecol.* 3: 2. <https://doi.org/10.1186/s40462-015-0030-0>.
- Weaver J.L. 1993: Refining the equation for interpreting prey occurrence in gray wolf scats. *J. Wildl. Manag.* 57: 534–538.
- Whitehouse-Tedd K., Wilkes R., Stannard C. et al. 2020: Reported livestock guarding dog-wildlife interactions: implications for conservation and animal welfare. *Biol. Conserv.* 241: 108249. <https://doi.org/10.1016/j.biocon.2019.108249>.
- Young J.K., Olson K.A., Reading R.P. et al. 2011: Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. *Bioscience* 61: 125–132.