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Identification of land predators of African Penguins *Spheniscus demersus* through post-mortem examination

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The African Penguin *Spheniscus demersus* is an endangered seabird endemic to southern Africa, and killing sprees by terrestrial predators have been one of the main threats for its mainland colonies. The methods employed to manage predators may differ depending on the species involved, therefore the implementation of strategies to limit the impacts of predation relies on the correct identification of the culprit predator. We report and quantify the lesions seen in African Penguins killed by four species of terrestrial predators: Caracal *Caracal caracal* (52 kills), Leopard *Panthera pardus* (27 kills), Domestic Dog *Canis lupus familiaris* (10 kills), and Cape Grey Mongoose *Galerella pulverulenta* (4 kills). We discuss patterns of necropsy findings that can be used to identify the predator species involved. Traditional forensic methods are useful tools to direct species-specific management actions for the conservation of the African Penguin and other seabirds so that effective mitigating measures can be deployed quickly to prevent further losses. It should be borne in mind, however, that the age, size and previous hunting experience of the predator are likely to influence the pattern of lesions that will be observed, and not all carcasses will have hallmark lesions or recognisable bite marks.

Identification des prédateurs terrestres de Penguins d'Afrique *Spheniscus demersus* par examen post mortem

Le Manchot Africain *Spheniscus demersus* est un oiseau de mer en voie de disparition endémique de l'Afrique australe, et les tueries perpétrées par les prédateurs terrestres ont été l'une des principales menaces pour ses colonies continentales. Les méthodes utilisées pour gérer les prédateurs peuvent varier en fonction des espèces impliquées. La mise en œuvre de stratégies visant à limiter les effets de la prédation repose de ce fait sur l'identification correcte du prédateur coupable. Nous rapportons et quantifions les lésions observées chez des Manchot Africains tués par quatre espèces de prédateurs terrestres: Caracal *Caracal caracal* (52 attaques), Léopard *Panthera pardus* (27 attaques), Chien Domestique *Canis lupus familiaris* (10 attaques), et Mangouste Gris *Galerella pulverulenta* (4 attaques). Nous discutons des modèles de résultats de nécropsie qui peuvent être utilisés pour identifier les espèces prédatrices impliquées. Les méthodes médico-légales traditionnelles sont des outils utiles pour orienter les actions de gestion spécifiques à une espèce pour la conservation du Manchot Africain et d'autres oiseaux de mer, de sorte que des mesures d'atténuation efficaces puissent être déployées rapidement pour éviter de nouvelles pertes. Il convient toutefois de garder à l'esprit que l'âge, la taille et l'expérience de la chasse du prédateur auront probablement une influence sur le type de lésions observées, et toutes les carcasses ne porteront pas de lésions caractéristiques ni de marques de morsure reconnaissables.

Keywords: carcasses, carnivores, necropsy, predation, South Africa, Spheniscidae, terrestrial predators, wildlife conflict

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Introduction

The African Penguin *Spheniscus demersus* is endemic to the Agulhas–Benguela upwelling region of southern Africa (Crawford et al. 2013). Population numbers decreased by more than 95% since the start of the 20th century, and the species is currently assessed as Endangered, with a remaining global population of approximately 25 000 breeding pairs (Nel et al. 2003; Crawford et al. 2011; BirdLife International 2018). The recent decline in numbers has mainly been attributed to reduced availability of food, resulting primarily from shifts in the distribution of prey species and competition with commercial fisheries and fur seals (Crawford et al. 2011, 2013). Given the sharp population decrease during the last century and the ongoing threats to African Penguins, there is concern regarding the long-term viability of the species in the wild (Department of Environmental Affairs 2013; BirdLife South Africa 2016).

Historically, with the exception of two small colonies at coastal caves in Namibia (Kemper 2015), the breeding colonies of African Penguins were exclusively located on islands. However, since the 1980s there have been a number of attempts by penguins to establish new colonies on the mainland (Whittington et al. 1996; Crawford et al. 2000). In South Africa, failed attempts occurred in 1981 at Cape Recife, in 1982 at Lambert's Bay harbour (Loutit and Boyer 1985; Whittington et al. 1996), and in 2003 at De Hoop (Underhill et al. 2006; Crawford et al. 2008). In contrast, the attempts to establish colonies in 1982 at Stony Point and in 1985 at Boulders were successful, and these colonies have flourished while most island colonies declined (Whittington et al. 1996; Crawford et al. 2000; Underhill et al. 2006). The numbers of penguins currently breeding at Boulders (inclusive of the Boulders section of the Table Mountain National Park as well as the contiguous colony area in Simon's Town) and at Stony Point were estimated at about 850 pairs and 2 000 pairs in 2016, respectively (Department of Environmental Affairs, unpubl. data), representing approximately 32% of the penguin population in the Western Cape Province and 18% of the total South Africa population (Crawford et al. 2013; BirdLife International 2018). Positive trajectories in population numbers at these colonies have partially been attributed to their favourable location in relation to the eastward shift in the distribution of main prey species and limited commercial fishing activities in the surrounding areas (Crawford et al. 2011; Sherley et al. 2014).

However, terrestrial predators can be an important pressure for this species' mainland colonies. This was illustrated by the impact that predation by Leopard *Panthera pardus* had on Stony Point in the late 1980s and early 1990s, when a series of killing sprees led to the death of more than 130 penguins (at the time, the colony had ~139 pairs) (Whittington et al. 1996) and by the fact that the De Hoop colony (~18 pairs) became extinct due to a single killing spree by Caracal *Caracal caracal* (Crawford et al. 2008; BirdLife South Africa 2016). The Boulders and Stony Point colonies are located within residential areas, suggesting that, even if this places them at an increased risk of predation by domestic dogs and cats, human presence and urbanisation provide partial relief from the pressure exerted by wild terrestrial predators (Petersen et al. 2006). Despite this, the pressure exerted by terrestrial predators seems to have increased in recent years (subj. obs.), with the penguin-monitoring programme and local park rangers reporting 50 and 138 penguins killed by terrestrial predators in 2015 and 2016, respectively, at Boulders (SANParks and City of Cape Town, unpubl. data), and 341 and 217 penguins killed in the same years at Stony Point (CapeNature, unpubl. data).

Many predators can kill African Penguins on land (Table 1), and the methods employed to manage predators differ depending on the target species. Therefore, the strategies to limit the impacts of predation rely on the correct identification of the predator. Forensic pathology can be a valuable tool to determine the predator species through the examination of lesions, carcass consumption patterns, and bite marks (Ratz and Moller 1997; Ratz et al. 1999; Lyver 2000; Cuthbert 2003); however, these methods have yet to be employed for African Penguins. In this study, we report and quantify the lesions found in carcasses of African Penguins killed by four species of terrestrial predators at mainland colonies in South Africa: Caracal, Leopard, Domestic Dog *Canis lupus familiaris*, and Cape Grey Mongoose *Galerella pulverulenta*.

Materials and methods

Penguin carcasses found at Stony Point (34°22′26″ S, 18°53′41″ E) and Boulders (34°11′50″ S, 18°27′04″ E) were submitted by local authorities to the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB) for post-mortem examination. Seven predation incidents from 2015 to 2017 where the predator species was established with a high degree of confidence, based on the capture of the individual predator or based on corroborating field evidence (such as sightings, camera traps, footprints or scats), were considered in this study (Figure 1; Table 2). Field evidence was interpreted by experienced park rangers and colony managers, being informed by field guides for the identification of spoors and scats of southern African mammals (Liebenberg 1990; Murray 2011).

For logistical reasons, not all carcasses could be obtained; a subset of 52 penguins that were killed by Caracal, 27 penguins killed by a Leopard, 10 penguins killed by Domestic Dogs, and 4 penguins killed by Cape Grey Mongoose were evaluated. Carcasses were examined following standard necropsy protocols (Hocken 2002) by experienced veterinarians (NJ Parsons and RET Vanstreels), and macroscopic lesions were noted. Penguins were differentiated according to age, as chicks (nestlings, with downy plumage still present), juveniles (plumage with a bluish or greyish tone and lacking well-defined bands) or adults (plumage with well-defined black and white bands) (Williams 1995). Ante-mortem and post-mortem tissue damage were differentiated based on the presence of vital response (e.g. haemorrhage, congestion, swelling) on the margins of the lesion and surrounding tissues (Dettmeyer et al. 2013). Unfortunately, in most cases the bite marks (puncture marks of canine teeth) from penguin carcasses were not measured and documented in sufficient detail to allow for detailed quantitative analyses.

Table 1: Known and potential predators of the African Penguin *Spheniscus demersus*

Species	References
Predators on land	
Mole Snake *Pseudaspis cana* (only on eggs)	1
Kelp Gull *Larus dominicanus* (only on eggs and chicks)	2, 3
Sacred Ibis *Threskiornis aethiopicus* (only on eggs and chicks)	3
Domestic Cat *Felis silvestris catus* (only on chicks)	3, 4
Cape Grey Mongoose *Galerella pulverulenta* (only on chicks)	5, 24
Domestic Dog *Canis lupus familaris*	6, 24
Caracal *Caracal caracal*	7, 24
Leopard *Panthera pardus*	6, 7, 24
Marsh Mongoose *Atilax paludinosus*	8
Cape Clawless Otter *Aonyx capensis*	7, 8
Cape Fur Seal *Arctocephalus pusillus pusillus*	9
Predators at sea	
Cape Fur Seal *Arctocephalus pusillus pusillus*	4, 10–13
Great White Shark *Carcharodon carcharias*	14–16
Killer Whale *Orcinus orca*	17, 18
Potential/incidental predators or scavengers	
Bryde's Whale *Balaenoptera edeni*	19
Copper Shark *Carcharhinus brachyurus*	16
Dusky Shark *Carcharhinus obscurus*	16
Large-spotted Genet *Genetta tigrina*	7
Cape Fox *Vulpes chama* (only on eggs and chicks)	6
Black-backed Jackal *Canis mesomelas*	20, 21
Brown Hyena *Hyaena brunnea*	22
Rat *Rattus* sp. (only on eggs and chicks)	23

References: (1) Underhill et al. 2009; (2) Berry et al. 1974; (3) Cooper 1974; (4) Apps 1983; (5) Crawford et al. 1995; (6) Whittington et al. 2000; (7) Whittington et al. 1996; (8) CapeNature, unpubl. data; (9) Rebelo 1984; (10) Shaughnessy 1978; (11) Marks et al. 1997; (12) Crawford et al. 2001; (13) Du Toit et al. 2004; (14) Bass et al. 1975; (15) Johnson et al. 2006; (16) Randall et al. 1988; (17) Randall and Randall 1990; (18) Williams et al. 1990; (19) Olsen 1913; (20) Loutit and Boyer 1985; (21) Avery et al. 1987; (22) Siegfried 1984; (23) Frost et al. 1976; (24) current study

Figure 1: Camera trap photograph of a Caracal *Caracal caracal* killing an adult African Penguin *Spheniscus demersus*. Photo credit: City of Cape Town

Additionally, canine measurements and bite mark impressions of known and potential predators of African Penguins were produced from specimens of the collection of the Iziko South African Museum (Cape Town, South Africa), and these methods and results are provided in the online supplementary material.

Results

Lesions associated with predation by Caracal

Penguin carcasses preyed upon by Caracal corresponded to 52 individuals (1 chick, 9 juveniles, and 42 adults), representing a subset of the 294 individuals killed during three killing sprees at Boulders and Stony Point (Table 2). Based on the patterns of lesions observed during necropsy, these cases were subjectively classified in three categories (Table 3): no external wounds, only neck punctures, and neck consumed.

The 'only neck punctures' category was most frequent (31 cases, 60%) and comprised carcasses that externally had only puncture wounds (or relatively small tear wounds) to the back of the skull or the upper neck, but lacked more extensive external wounds. Based on the size of the puncture wounds (diameter 1.8–5.0 mm) and their arrangement in pairs (distance 12–25 mm), these were considered consistent with bite marks (Appendix 1D–F). The soft tissues underlying these bite marks showed varying levels of trauma, ranging from minor hematomas to extensive tearing of muscles and haemorrhage (Appendix 1G–I). The number of bite marks or their external appearance did not necessarily reflect on the amount of damage to the underlying tissues, and in many cases even relatively small bite marks led to massive

Table 2: Overview of the predation incidents of African Penguins that were evaluated in this study

Predator	Location	Period	Penguins killed	Penguins necropsied	Remarks
Caracal	Boulders	22 Jun–8 Jul 2016	42	6	Footprints and scats consistent with Caracal were found in the colony. Traps were set and an adult female Caracal was captured on 8 July 2016, with no further predator-related deaths of penguins being recorded in the following months.
Caracal	Boulders	21 Aug 2016–11 Oct 2017	213	7	Camera traps confirmed the presence of a Caracal in the colony, including some instances where the killing of penguins was documented through photographs. Traps were set and a sub-adult male Caracal was captured in 11 October 2017, with no further predator-related deaths recorded in the following months.
Caracal	Stony Point	25 Aug–12 Oct 2016	39	39	Camera traps confirmed the presence of two Caracals (sub-adult and adult) in the colony in the nights of the killing. Traps were set and a sub-adult male Caracal was captured on 2 September 2016, and an adult female Caracal was captured on 12 October 2016, with no further predator-related deaths recorded in the following months.
Leopard	Stony Point	11 Jun 2016	31	27	An adult male Leopard was seen leaving the colony in the morning. One carcass was entirely consumed (only a pelt of skin and feathers remained), and the remaining carcasses were placed in small piles of 3 to 5, apparently hoarded for later consumption. Adaptive deterrence measures (acoustic, olfactory and visual aids) were introduced for a two-week period following the incident and no further predator-related deaths of penguins were recorded in the following months.
Domestic Dog	Boulders	25 Sep 2015	22	10	Based on footprints present around penguin carcasses, it was concluded that two domestic dogs had been involved (footprint widths of 6 and 8 cm); however, the dogs were never identified but apparently did not return to the area.
Cape Grey Mongoose	Stony Point	21 Oct–6 Nov 2015	3	3	A small group (3 or 4 individuals) of Cape Grey Mongoose was seen entering the colony on several evenings during the period. In one instance, the group was seen attacking a medium-sized downy chick and dragging it away into the bushes, where it was killed out of sight. Cape Grey Mongoose faeces were found in the area and contained penguin feathers. Traps were set and an adult Cape Grey Mongoose was captured.
Cape Grey Mongoose	Stony Point	24 Oct 2016	1	1	The killing was not witnessed, but Cape Grey Mongoose footprints and faeces containing penguin feathers were found in the area.

internal damage (Appendix 1I). The bite marks were mostly concentrated near to the ear, at the junction of the jaw and the upper neck, with damage either to the ventral or dorsal part of the neck. Dissection of the skull revealed that in most cases the superior sagittal sinus surrounding the cerebellum (and sometimes extending towards the cerebrum) was markedly haemorrhagic, and the dissection of the occipital joint also frequently revealed substantial subdural haemorrhage in the cervical spinal cord; the brain itself did not present significant lesions or haemorrhage (Appendix 1J). In some cases, the bite wounds were relatively deep (~2–3 cm) and had caused extensive damage to the core of the neck. At times, the jugular veins were ruptured, causing large subcutaneous haematomas. In other cases, however, the wounds were superficial (<1 cm deep) and lacked the depth to cause direct spinal cord damage; hence, the spinal damage was presumed to have been indirect, perhaps through the luxation of the cervical joints by violently shaking or forcefully twisting the neck. This was corroborated by the fact that vertebral luxation could often be felt through palpation, particularly of the atlanto-axial joint.

The 'neck consumed' category was relatively common (18 cases, 35%) and comprised cases where there was post-mortem tearing of the skin to consume the soft tissues and vertebrae of the neck (Appendix 1K). Cervical muscles and vertebrae were chewed upon starting on the upper neck and progressing towards the pectoral girdle; back and keel muscles were also consumed in some cases, and the anterior margin of the keel bone was occasionally chewed upon. Other soft tissues of the neck (e.g. oesophagus and trachea) were consumed at times but did not appear to be preferentially targeted. None of the cases showed any consumption of viscera from the body cavity. Depending on the level of consumption, the carcass was near-decapitated (Appendix 1K) or completely decapitated (Appendix 1L). In most cases of complete decapitation, where the head was found in an adjacent area, there was no evidence of chewing or consumption of the skull.

The ‘no external wounds’ category was the least frequent (3 cases, 6%) and corresponded to cases where there was significant subcutaneous and muscular bruising to the back of the head and upper neck despite the absence of perforating or tearing wounds. In addition to the subcutaneous and muscular lesions, further dissection revealed that the superior sagittal sinus of the cerebellum and caudal cerebrum was markedly haemorrhagic, and there was substantial subdural haemorrhage surrounding the cervical spinal cord.

Lesions associated with predation by Leopard

Twenty-seven adult penguins predated by Leopard were examined, representing a subset of the 31 individuals killed during a killing spree by a single Leopard at Stony Point (Table 2). Externally, most affected individuals only showed small amounts of blood on the neck, and in most cases there was no tearing or consumption of the carcass. Based on the patterns of lesions observed upon external examination, cases were subjectively classified in three categories (Table 4): no neck fracture, single neck fracture, and multiple neck fractures.

All of these cases had puncture wounds on the lower neck or upper back, which based on their size (diameter 5–15 mm) and arrangement in pairs (distance 25–40 mm) were considered consistent with bite marks (Appendix 2C). These bite marks were frequently accompanied by extensive tearing and bruising of the underlying soft tissues (Appendix 2D), and in most cases were accompanied by fracture of one vertebra (22 cases, 81%), but less often by multiple vertebral fractures (3 cases, 11%). These bite marks and fractures occurred primarily in the lower parts of the neck, on the dorsal aspect. Accordingly, vertebral fractures occurred predominantly on the lower and mid-neck. In a small number of cases, the jugular veins and/or the trachea were also severed. Additional bite marks were seen less frequently on the chest and/or on the lower back and flanks, leading to substantial muscular damage; the lack of significant haemorrhaging, however, suggests that these lesions were inflicted post-mortem (Appendix 2E, F). Conversely,

Table 3: Necropsy findings of African Penguins killed by Caracal

Necropsy findings	No external wounds (*n* = 4)	Only neck punctures (*n* = 31)	Neck consumed (*n* = 17)	Total (*n* = 52)
Complete decapitation	0	0	33%	12%
Near-decapitation or extensive tearing and consumption of the neck	0	0	67%	23%
Puncture wounds consistent with bite marks to the head or upper neck	0	90%	11%	58%
Puncture/tear wounds not clearly attributable to bite marks	0	29%	28%	27%
Significant subcutaneous and muscular damage to the head or upper neck	67%	100%	39%	77%
Wounds or bruises consistent with blunt trauma or claw strikes to the body	33%	39%	11%	29%
Skull/cervical luxation or relatively minor fracture, with spinal cord damage	100%	90%	0	60%
One or both jugular veins ruptured	0	32%	6%	21%
Lung severely congested and/or blood in air sacs	0	29%	28%	27%
Crushing or perforation of trachea	0	16%	6%	12%
Blood in mouth or trachea	33%	29%	6%	21%
Intestinal perforation or rupture	0	3%	0	2%

Table 4: Necropsy findings of African Penguins killed by Leopard

Necropsy findings	No neck fractures (*n* = 2)	Single neck fracture (*n* = 22)	Multiple neck fractures (*n* = 3)	Total (*n* = 27)
Fracture of an upper neck vertebra, C1–C4	0	9	0	7%
Fracture of a mid-neck vertebra, C5–C8	0	27	100%	33%
Fracture of a lower neck vertebra, C9–C13	0	64%	100%	63%
Puncture wounds consistent with bite marks to the neck or upper back	100%	100%	100%	100%
Puncture wounds consistent with bite marks to the chest	50%	9%	0	11%
Puncture wounds consistent with bite marks to the lower back or flank	0	14%	0	11%
Extensive subcutaneous and muscular damage to the neck	50%	59%	33%	56%
One or both jugular veins ruptured	100%	41%	0	41%
Perforation or tearing of trachea	50%	23%	0	22%
Aspiration pneumonia	0	14%	0	11%
Lung severely congested/haemorrhagic and/or blood in air sacs	50%	36%	100%	44%
Bruising or tear wounds to the flank or chest	50%	32%	0	30%
Intestinal rupture	0	9%	0	7%

ante-mortem bruising and tear wounds to the body were seen in some cases (6 cases, 22%). Intestinal rupture due to blunt force trauma to the abdomen and the presence of food material in the lungs (aspiration pneumonia) were also recorded in a small number of carcasses (2 and 3 cases, respectively). It was subjectively noted that lesions to the thorax and abdomen were more frequent in carcasses with no or a single neck fracture (see Table 4).

Lesions associated with predation by Domestic Dog

Carcasses of 10 penguins (1 chick, 2 juveniles, and 7 adults) preyed upon by Domestic Dogs were examined, representing a subset of the 22 individuals killed during a killing spree at Boulders (Table 2). With the exception of one case, where there were no puncture or tear wounds to the skin, all penguins preyed upon by Domestic Dogs had one or more wounds on the lower body (especially the abdomen and inguinal area) (Table 5). Some of these wounds bore resemblance to bite marks, but in many cases they were single puncture wounds or wounds that were not distributed in pairs that could be recognised as being related to canine marks (Appendix 3E, F). In most cases there was extensive subcutaneous and muscular haemorrhage underlying these skin wounds (Appendix 3G–I). Subcutaneous and muscular bruising was also seen in areas where there were no skin wounds, suggesting that a dog's teeth were not able to penetrate the skin and/or that the damage had been caused by blunt force trauma (e.g. pouncing, 'death shake,' or paw anchoring/stamping of the penguin's body).

Crushed and haemorrhagic lungs and kidneys were recorded in nearly all confirmed cases of Domestic Dog predation, leading to substantial accumulation of blood in the air sacs, mouth and trachea, and in the kidney capsule and surrounding soft tissues, often resulting in large retro-coelomic blood clots. These lesions were sometimes the direct result of puncture and tear wounds to the back, but more frequently the puncture wounds did not penetrate deep enough to account for the damage to these internal organs, and therefore probably resulted from blunt-force trauma. Only one carcass had been partially consumed post-mortem, with the skin and muscles of the upper back having been torn.

Lesions associated with predation by Cape Grey Mongoose

Four penguin chicks predated by Cape Grey Mongoose were examined from two predation incidents at Stony Point (Table 2). In all four cases, the dorsal skin had been torn and removed from the head towards the upper back, with the underlying muscles and vertebrae consumed to varying degrees. None of the cases presented puncture wounds that could be attributed to bite marks. In one case, the skin had been torn down to the upper chest. In three cases, the cervical vertebrae had been chewed upon, and in two of these cases, this led to a near-decapitation or complete decapitation. In two cases, the back of the skull had been fractured and the brain and cerebellum were consumed (Appendix 4C); in another case, the skull was not cracked open but the occipital muscles had been removed and the skull was scratched (Appendix 4B), presumably by attempts to open it. Severe lung congestion was noted in three of the cases.

Discussion

Although some predation events were directly documented (e.g. Figure 1), in most cases the predation was not directly witnessed and the identity of the predator remain uncertain. Nonetheless, because the cases included were those where the predator species could be established with a high degree of confidence based on field evidence (sightings, camera traps, footprints or scats) as observed by experienced field rangers, the identity of the predator species was considered reliable. Although the possibility exists that secondary predators or scavengers could have interfered with the carcasses leading to misinterpretation of the lesions, this was unlikely because the study colonies were monitored on a daily basis and the carcasses were rapidly removed. Furthermore, there were no indications that the carcasses had been visited by scavengers (e.g. spoors, secondary sets of bite marks, etc.).

The lesions observed in carcasses of African Penguins that had been killed by terrestrial predators follow some general patterns in the necropsy findings, dependent on the predator species involved (Table 6). In combination with field evidence collected by park rangers (spoors, scats, signs of struggle, camera traps, etc.), these patterns can be useful to differentiate species in cases where the culprit predator is unknown, informing the implementation of species-specific mitigation measures. Several studies and field guides have been published for the identification of southern African predators involved in the killing of livestock employing similar methods, and may provide useful information for the identification of predators of seabirds (Roberts 1986; Hodkinson et al. 2007; Smuts 2008).

The killing techniques employed by Caracal and Leopard to kill African Penguins were consistent with those used by these predators to kill small antelope, resulting in relatively 'clean' kills with few bite marks to the neck (Kingdon and Hoffmann 2013). A similar killing technique appears to be employed by Cougar *Puma concolor* in Argentina, based on camera-trap photographs showing cougars carrying Magellanic Penguins *Spheniscus magellanicus* by holding them with a bite to the upper neck (Frere et al. 2010). Caracal primarily targeted the upper (cranial) parts of the neck, whereas the Leopard preferred the lower (caudal) neck; but perhaps the most reliable parameter to differentiate predation by these predators is the size and inter-canine spread of the bite marks and the greater force exerted that is observed in cases of Leopard predation. In carcasses where no canine puncture marks were found because the skin had been torn out or consumed, Caracal involvement can be determined by the characteristic pattern of near-decapitation or decapitation due to the chewing of neck muscles and vertebrae down to the pectoral girdle, which was not seen in Leopard-predated carcasses. However, it should be borne in mind that decapitation and near-decapitation was also seen in penguin chicks killed by Cape Grey Mongoose.

The lesions reported in cases of Domestic Dog predation of Blue Penguins *Eudyptula minor* and Yellow-eyed Penguins *Megadyptes antipodes* in New Zealand are nearly identical to those seen in this study, comprising extensive bleeding from the mouth and extensive internal damage due to the crushing of the chest and intrapulmonary bleeding (Hocken 2000, 2002, 2005). It is not unusual for there to be no external puncture wounds even though extensive subcutaneous bruising is present, suggesting that dogs' teeth often do not penetrate the skin of penguins (Hocken 2000, 2002, 2005). In addition to the extensive lung damage that was seen in almost all dog-predated carcasses in this study, the kidneys were also extensively damaged in all cases, which corroborates that penguins attacked by dogs suffer extensive blunt-force trauma to the back. Although no such instances were recorded in this study, groups of dogs are known to occasionally engage in a 'killing frenzy' behaviour, wherein they bite each penguin once, shake it violently ('death shake'), and then drop it and move on to attack the next penguin; in these cases, recognisable bite marks would be present on the penguin's back or neck (Hocken 2002). In addition to the lesions on the carcasses, it would seem that the characteristically 'messy' kills with abundant signs of struggle can be particularly useful to identify dog predation.

The lesions documented in cases of predation by Cape Grey Mongoose were similar to those reported for Stoat *Mustela erminea* and Ferret *Mustela putorius furo* predation of Blue Penguins and Yellow-eyed Penguins in New Zealand (Hocken 2000, 2002, 2005). In these cases, the sub-occipital region was also the primary area of target, and carcass consumption was initiated by consuming the neck muscles and vertebrae from the upper neck towards the pectoral girdle, occasionally leading to decapitation. Penguins preyed upon by mustelids in New Zealand often have small but recognisable bite marks (Ratz et al. 1999; Hocken 2000, 2002), a characteristic that was not seen in this study. It is possible, however, that the sections of the skin where the puncture wounds would have been present in this study were removed during the consumption of the carcasses. It is also interesting to note that the Cape Grey mongooses in this study were able to fracture and open the skull of African Penguin chicks, whereas Stoats and Ferrets did not appear to do so when feeding on Blue Penguins and Yellow-eyed Penguins (Hocken 2000, 2002).

Table 5: Necropsy findings of African Penguins killed by Domestic Dogs

Necropsy findings	Frequency (*n* = 10)
Absence of puncture or tearing wounds	10%
Puncture or tear wounds to the back	30%
Puncture or tear wounds to the flanks or flippers	40%
Puncture or tear wounds to the abdomen or inguinal area	70%
Subcutaneous bruising to the back	50%
Subcutaneous bruising to the flanks	70%
Subcutaneous bruising to the abdomen or inguinal area	60%
Lungs diffusely haemorrhagic and crushed	90%
Kidneys diffusely haemorrhagic and crushed	100%
Blood in mouth or trachea	100%
Blood in air sacs	80%
Blood in coelomic cavity	10%
Fracture of caudal ribs	10%
Consumption of skin and muscles of the upper back	10%

Table 6: Comparison of the predator-specific necropsy findings documented in African Penguin

Characteristics	Caracal	Leopard	Domestic Dog	Cape Grey Mongoose
Penguin age group targeted	Mostly adults	Adults	Mostly adults	Chicks
Primary attack area	Throat, upper neck	Lower neck	Lower body	Head, upper neck
Consumption of carcasses	Neck, upper back, upper chest	Upper chest	Upper back	Skull, upper neck
Presence of bite marks	Usually present, readily recognisable canine punctures	Usually present, readily recognisable canine punctures	Occasionally present, variable in shape and size	Not present or not recognisable
Upper canine distance	24–30 mm[a]	40–46 mm[b]	28–60 mm[a]	
Hallmark lesions	Bite marks near the ear, with subcutaneous and muscular bruising and spinal cord damage; consumption of neck muscles and vertebrae leading to decapitation	Bite marks on the base of the neck, massive lower neck trauma, with muscular bruising and crushing of vertebrae	Diffuse subcutaneous and muscular bruising to the back and flanks, leading to haemorrhage and crushing of lungs and kidneys	Chewing and consumption of the muscles of the upper neck and skull, fracturing of the skull and consumption of the brain

[a] Roberts (1986); [b] Cheetah Conservation Botswana (2012)

When identifying the predator species responsible for penguin deaths, it is important to consider that the age and size of the predators and its previous hunting experience are likely to influence the pattern of lesions that will be observed. Especially for felids, young or inexperienced individuals are likely to produce 'messy' kills, with signs of struggle and numerous sub-lethal injuries, whereas more-experienced individuals are likely to kill efficiently and with minimal struggle. For instance, the authors have witnessed cases of predation of African Penguins by a Domestic Dog at Robben Island which showed a more-efficient killing technique with most attacks directed at the neck and head, producing 'cleaner' kills (NJ Parsons, unpubl. data). In this context, it should be noted that only predation by a single Leopard was documented; and it is, therefore, possible that different patterns of lesions might occur if individuals with greater or lesser experience are involved. Furthermore, when investigating predator killing sprees it should be borne in mind that not all carcasses will have hallmark lesions or recognisable bite marks, and the post-mortem examination might be inconclusive for some of the carcasses. For this reason, it is recommended that all available carcasses should be examined since at least some of them will have enough diagnostic features to allow for the identification of the predator.

A detailed analysis of bite marks (puncture marks of canine teeth) was unfortunately not conducted. Previous studies have shown that bite-mark analysis can be a valuable tool to identify predators of wild animals (Ratz and Moller 1997; Ratz et al. 1999; Lyver 2000), and this technique could potentially be useful in the case of the African Penguin. Employing museum specimens, bite-mark impressions and canine measurements have been provided in the online supplementary material, which will hopefully be useful in future research for the identification of African Penguin predators. Another method to posthumously identify culprits of predation is the detection of DNA from saliva collected from the bite wounds of the prey (Blejwas et al. 2006; Sundqvist et al. 2008; Wengert et al. 2013). This method has been applied to the identification of predators of marine mammals (van Bleijswijk et al. 2014; Leopold et al. 2015) and could be valuable for future research on the predators of penguins. However, while molecular methods may improve the diagnosis accuracy and have great potential from a research perspective (and for legal purposes), the identification of predators based on field evidence and post-mortem examinations of lesions has the advantage of lower costs and less time requirements. Considering that tens of penguins may be killed per night when a terrestrial predator is on a killing spree, waiting a few days for laboratory results before deploying traps or implementing deterrence measures might not be suitable for conservation management purposes.

In conclusion, the gregarious habits and limited terrestrial agility of African Penguins, possibly combined with a lack of appropriate behavioural responses and defence mechanisms, render them vulnerable to predation by terrestrial predators. Managing the pressure exerted by terrestrial predators will therefore be critical to ensure the persistence of mainland colonies. Furthermore, a potential conservation strategy currently under consideration is the artificial establishment of new African Penguin breeding colonies on the mainland, in parts of the South African coast where spawning forage fish are abundant but no coastal islands are present (Department of Environmental Affairs 2013; BirdLife South Africa 2016). Considering the impact that terrestrial predators can have on mainland colonies, particularly during the early stages of colonisation, preventing and mitigating predation will have to be a key component in this conservation strategy. And because the implementation of measures to limit the impacts of killing sprees relies on the correct identification of the predator species involved, forensic pathology and bite-mark analysis can be valuable tools to inform conservation management of this species.

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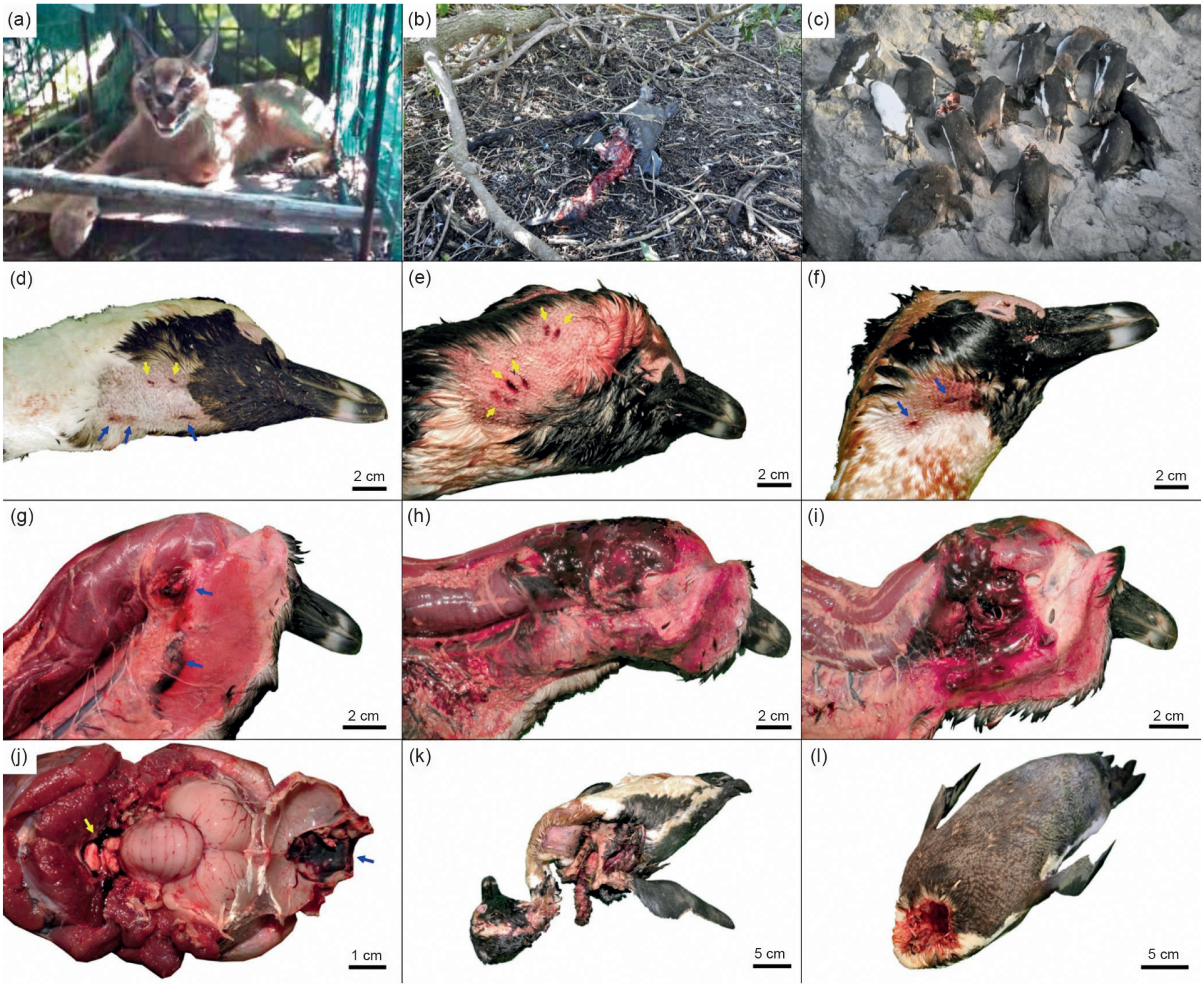
Appendix 1: Field evidence and lesions of African Penguins *Spheniscus demersus* killed by Caracal *Caracal caracal* in South Africa

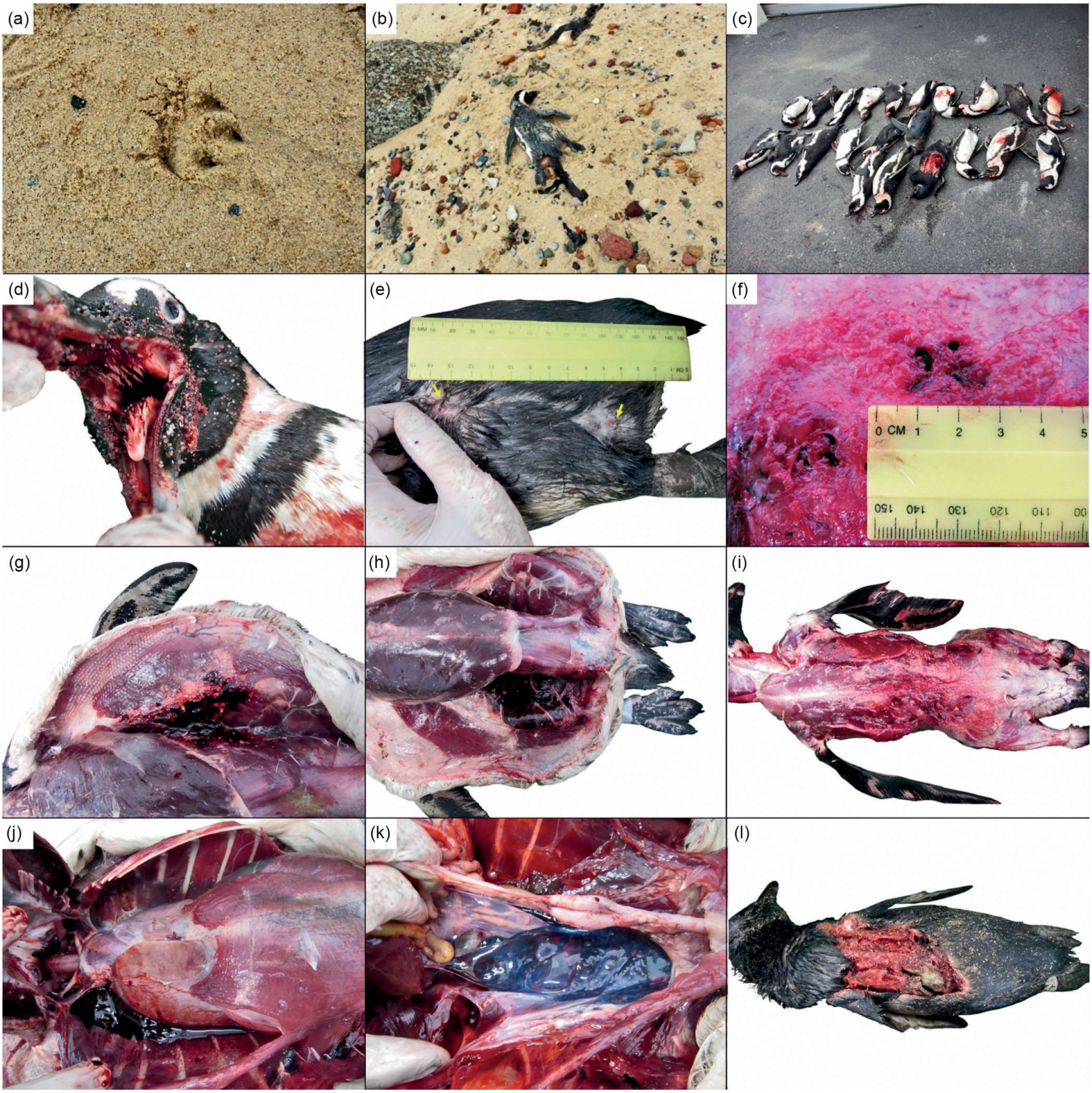


(a) A Caracal captured at Stony Point; (b) penguin killed and partially consumed by a caracal at Boulders; (c) surplus killing of 14 penguins by two Caracals at Stony Point (carcasses were artificially grouped for the photograph); (d, e, f) puncture wounds consistent with bite marks of the mandibular canines (yellow arrows) and maxillary canines (blue arrows) (feathers were cut away to show the wounds); (g subcutaneous and muscular bruising to the neck (blue arrows) in a case where there no external wounds; (h, i) extensive subcutaneous and muscular bruising and tearing to the neck; (j) haemorrhagic superior sagittal sinus dorsal (blue arrow) and subdural cervical spinal cord haemorrhage (yellow arrow); (k) near-decapitation, where the cervical vertebrae and the soft tissues of the neck and upper body were consumed but the head remains attached to the body by a strip of skin; (l) complete decapitation, where the head and neck are missing and the soft tissues and vertebrae of the upper body were partly consumed. Photo credits: (a, c) Cuan McGeorge/CapeNature; (b) City of Cape Town; (d–l) Ralph ET Vanstreels

Appendix 2: Field evidence and lesions of African Penguins *Spheniscus demersus* killed by a Leopard *Panthera pardus* in South Africa

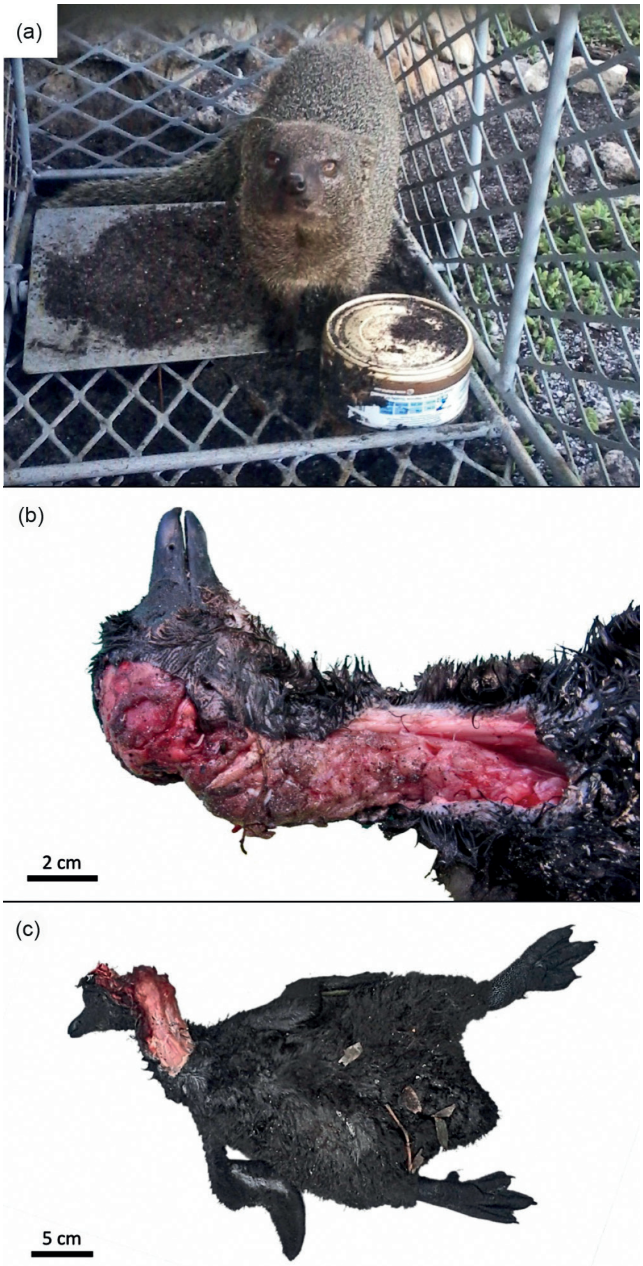
(a) Leopard photographed at Stony Point; (b) penguins that were killed but not consumed by a Leopard (the carcasses were found in small groups, apparently having been hoarded by the predator); (c) puncture wounds consistent with bite marks (arrows); (d) extensive subcutaneous and muscular bruising and tearing to the neck; (e, f) extensive tearing of the anterior parts of the keel muscles. Photo credits: (a) Van As Jordaan; (b) CapeNature; (c–f) Nola J Parsons

Appendix 3: Field evidence and lesions of African Penguins *Spheniscus demersus* killed by Domestic Dogs *Canis lupus familiaris* in South Africa



(a) Dog footprints near penguin carcasses; (b) penguin killed by Domestic Dog, surrounded by a large quantity of footprints and signs of struggle (i.e. 'messy' kill); (c) surplus killing of 22 penguins in a single night by two domestic dogs at Boulders (carcasses were artificially grouped for the photograph); (d) large quantities of blood emerging from the mouth; (e) puncture wounds consistent with bite marks (arrows); (f) puncture wounds consistent with bite marks, from a subcutaneous perspective; (g) extensive subcutaneous haemorrhage in the flank and scapular area; (h) extensive subcutaneous haemorrhage in the pelvic area and legs; (i) extensive subcutaneous haemorrhage and muscle tearing on the scapular area (the skin was removed to expose lesions); (j) large quantities of blood in the thoracic air sacs; (k) extensive retrocoelomic haemorrhage in the pelvic area; (l) consumed carcass, with the skin and muscles of the upper back having been torn and consumed. Photo credits: (a–c) SANParks; (d–l) Nola J Parsons

Appendix 4: Field evidence and lesions of African Penguins *Spheniscus demersus* killed by Cape Grey Mongoose *Galerella pulverulenta* in South Africa



(a) Cape Grey Mongoose captured at Stony Point; (b) tearing and consumption of the skin and muscles of the neck; (c) tearing and consumption of the skin and muscles of the neck, with fracturing of the skull and consumption of the brain and cerebellum. Photo credits: (a) CapeNature; (b, c) Nola J Parsons