LIFE ON THE EDGE: EXPLORING THE EFFECTS OF URBANISATION ON THE FORAGING ECOLOGY AND ECOTOXICOLOGY OF CARACALS

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DECLARATION

I, Gabriella Ruth Michaela Leighton, hereby declare that this thesis was carried out in accordance with the regulations of the University of Cape Town; that the work upon which this thesis is based is my original work (except where expressly indicated otherwise); and that neither the whole work nor any part thereof has been, is being, or is to be submitted for another degree at this or any other university. I grant the university free license to reproduce the contents for research in whole or in part. The cover artwork is copyrighted to the artist, Anya Ratnayaka, and my original artworks within the thesis are copyrighted to me. I am presenting this thesis for examination towards the Degree of Doctor of Philosophy in Biological Sciences.

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TABLE OF CONTENTS

ABSTRACT

The continuing loss of natural habitat to a broad range of human activities is one of the main drivers of biodiversity decline worldwide and a defining feature of the Anthropocene. However, some opportunistic, generalist species may benefit from transformed landscapes through, for example, the absence of apex predators or access to human-subsidised food resources. These benefits may thus offset the higher mortality and health risks typically associated with human-dominated landscapes. To understand the cost-benefit trade-offs of life on the urban edge, I investigated the foraging ecology and ecotoxicology of a highly adaptable medium-sized carnivore, the caracal (*Caracal caracal*), utilising both natural and transformed landscapes around the rapidly growing city of Cape Town, South Africa.

Through a combination of scat analysis (n = 654 scats) and prey remains located at 677 GPS clusters, I quantified dietary resource use of 26 collared individuals, as well as opportunistically sampled caracals. Using a range of gut transit times, I estimated whether scat at cluster sites was from the same or an earlier feeding event, thereby increasing the overall detection of individual-specific feeding events by > 50%. While most feeding events occurred within 200 m of the urban edge of Cape Town, I found that caracals have flexible diets that largely comprise medium- to small-sized wild prey (60%), followed by human-associated species (27%), and introduced or domestic species (13%).

Using a subset of the feeding and resting events (n = 326 prey remains, n = 384 scat, n = 177 resting sites) that were associated with known individuals (n = 17), I then investigated caracal resource selection using both anthropogenic and environmental factors. Additionally, I examined the behaviour of caracal at feeding clusters to determine if they respond to spatial and temporal risks associated with anthropogenic factors. I found divergent resource selection patterns based on the level of exposure to urbanisation: caracals living in the urban-dominated region of the Peninsula (n = 14; 548 feeding events) select for the urban edge, while caracals in the wildland-dominated region (n = 3; 162 feeding events) strongly avoid it. I argue that in the more urbanised region, caracals forage on or close to the urban edge because this is where the remaining low-lying wildland habitat is most productive and attractive. Consequently, caracals in heavily transformed areas, which might otherwise tend to avoid human disturbance, have habituated to human presence but reduce their risk of detection by remaining cryptic, prolonging handling time, and maintaining high feeding site fidelity where cover is available.

To quantify the consequences of peri-urban foraging, I use an ecotoxicological approach to assess environmental contamination and its potential effects on caracals. It is widely reported that persistent organic pollutants (POPs), including organochlorines (OCs) such as PCBs and DDT and its metabolites, are extremely toxic, causing adverse effects on wildlife and human health. I tested blood and adipose tissues of caracals, with different diets utilising a range of natural and transformed landscapes, for exposure to commonly detected OCs. Despite restrictions on their use, I found extensive OC burdens, with 100% of adipose samples exposed to both DDT and PCBs, and 100% and 83% of blood samples exposed to DDT and PCBs respectively. Caracals using areas with a higher density of people and electrical transformers, and those using areas close to informal settlements, had higher exposure to OCs. Additionally, the use of vineyards and wetlands and a diet with a greater proportion of higher trophic level or exotic prey correlated with a higher risk of exposure to OC pollutants. Full blood analyses revealed that exposure levels to OCs were also associated with higher counts of infection-fighting cells, suggesting these compounds may affect the immune response of individuals. With time, these detrimental effects may have population-level repercussions through impacts on reproductive success and fitness.

Together these findings reveal that while caracals and other medium-sized adaptable carnivores may persist within or adjacent to human transformed habitats, they still prefer natural habitat and pay a significant cost for foraging on prey species that have been contaminated by pollutants associated with urban and rural land uses. Urban edges may thus be an ecotoxicological trap, threatening the health and long-term persistence of caracals and other wildlife in this and other biodiversity hotspots. Reducing environmental contamination and limiting habitat loss to urban sprawl would benefit wildlife living on the transformed edges but requires significant improvements to both the legislation governing pollutants and the spatial planning of cities.

ACKNOWLEDGEMENTS

In tenui labor, at tenuis non gloria

(The object of the labour was small, but not the glory)

– Virgil, *Georgics IV.6* (29 B.C.)

In this poem, Virgil was referring to bees. The scientific endeavour relies on the cumulative efforts of many. While a doctorate is an isolating, solo undertaking, this thesis was made possible through the concerted input of many "bees". I am cognisant of the contributions of the scientists who have gone before me on whose work I drew so much, those people who helped my own research directly, and those in my life who may not have had a clue what I was doing but provided support, nonetheless.

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The journey to this point has not been without difficulties, both personal and external, not least being massive student protests resulting in disrupted work and access to campus (2015 – 2016), complete national lockdown due to the global COVID-19 pandemic (2020 – 2021), and a tragic, uncontrolled fire that damaged the iCWild lab in the H.W. Pearson building on Upper Campus (2021). I never anticipated there being quite so many dramatic ups and downs, despite being assured by so many people that there undoubtedly would be. I am grateful I was able to continue my work despite these trials and could be productive through lockdown when so many people could not. The "hive" of people and resources I am lucky to be surrounded by has not only made this PhD seem achievable, but also far less painful. In the immortal words of Douglas Adams, "So long, and thanks for all the fish".

Paintings depicting caracal necropsies shown at "….*from here*", a group exhibition on the 7th December 2016 at Spencer Street studio (now InSitu studio) in Cape Town, South Africa. CM17 (pre-necropsy) was a lactating female hit by a car and CM20 (post-necropsy) was a juvenile male trapped by a farmer.

G. R.M. Leighton *Caracal mortality 17* (2016), oil on canvas, 100 x 100 cm.

G. R.M. Leighton *Caracal mortality 20* (2016), oil on canvas, 102 x 76 cm.

CHAPTER 1

INTRODUCTION

URBAN ECOSYSTEMS

The Anthropocene is characterised by major land-use and climate change, precipitating wide-scale irreparable loss of biodiversity via the sixth mass extinction (Barnosky et al. 2011; Dirzo et al. 2014; Ceballos et al. 2015, 2017). Human disturbance of natural habitat and ecosystems is far-reaching and often irreversible, creating highly novel, unparalleled environmental conditions and systems concentrated around dense urban centres. These novel urban ecosystems dominate globally. More than half of all people now live in cities, with urban land cover expected to almost triple in area from 2000 to 2030 (Angel et al. 2005; Seto et al. 2012; United Nations 2018). This expansion is not uniform: while the rate of urbanisation in developed countries is slowing, it is accelerating in developing areas of Africa, Asia and Latin America (Seto et al. 2010; United Nations 2018), particularly for those countries in the Global South (Myers 2021). It is also troubling to note that the world's most rapidly growing cities fall within areas of high species diversity (Aronson et al. 2016; Venter et al. 2016), e.g., Cape Town, South Africa; Sao Paolo, Brazil; and Perth, Australia (Weller et al. 2018). Expanding urban areas therefore have profound ecological and evolutionary consequences for global biodiversity (Mcdonald et al. 2008).

On the leading edge of urban sprawl, species are increasingly forced into contact with both direct human presence and the products of the human footprint (i.e., development and habitat modification; Venter et al. 2016). Where wildlife face disturbances associated with cities, they must adapt to accommodate these novel stimuli, or locally perish. In an effort to avert a dramatic decay of biodiversity and the ensuing loss of ecosystem services, it is increasingly critical to understand how species communities respond to anthropogenic disturbance, particularly in those regions anticipating rapid environmental change (Magle et al. 2016; Gallo et al. 2017; Parsons et al. 2018) and the expansion of urban footprints.

WILDLIFE IN AND AROUND URBAN LANDSCAPES

Cities and their surrounding areas are loud (Kight and Swaddle 2011; Shannon et al. 2016), brightly lit (Dominoni et al. 2016, 2020), hot (Shochat et al. 2006; Heaviside et al. 2017), polluted (Dip et al. 2003; Serieys et al. 2015; Murray et al. 2019) and physically dominated by transportation routes and buildings (Crooks 2002; Riley et al. 2014c). Cities also harbour novel wildlife communities (Shochat et al. 2006), introduced and domestic species, and are associated with the emergence of new diseases that pose a risk to indigenous wildlife and humans (Bradley and Altizer 2007; Brearley et al. 2013; Becker et al. 2015). Together, all these disturbances interact to fundamentally disrupt ecosystem functioning (Shochat et al. 2010; McMahon et al. 2017; Dominoni et al. 2020). Wildlife that persists near urban areas often have restricted movement (Tucker et al. 2018; Ritzel and Gallo 2020), worse health (Murray et al. 2015, 2019) and high levels of anthropogenic

mortality (Hill et al. 2020b), e.g., from vehicle collisions (Seiler and Helldin 2006; Soulsbury and White 2015; Hill et al. 2020a), poaching (Kaltenborn and Brainerd 2016) and persecution (Inskip and Zimmermann 2009; Soulsbury and White 2015). Even seemingly low-impact recreational activities, such as hiking or cycling, can have adverse effects (Larson et al. 2016). When wildlife do not appropriately read and correctly respond to these novel challenges this mismatch can contribute to poorer health and mortality that have negative fitness outcomes, and ultimately lead to population declines in human-dominated landscapes (Sih 2013; Smith et al. 2021).

CARNIVORE ADAPTATIONS TO URBANISATION

URBAN FILTERING

Despite the diverse challenges to mobility, health and persistence presented by urbanisation, some animal species are poised to take advantage of opportunities that arise from anthropogenic disturbance and coexistence with humans (Suraci et al. 2021; Pineda-Munoz et al. 2021). In this way, cities can act as filters on ecological and life history traits that impart differential abilities to persist in transformed landscapes between and within species (Aronson et al. 2016; Santini et al. 2019). Urban filtering may result in biotic homogeneity around cities (McKinney 2002, 2006), although with some variation between populations, regions and taxonomic groups (La Sorte et al. 2007; Suraci et al. 2021). This reshaping of communities in ways that can be predicted from species traits, has important implications ranging from impacts on single-species conservation to broad-scale changes in patterns of ecosystem functioning (Estes et al. 2011; Schmitz et al. 2018; Suraci et al. 2021).

Multiple human activities can result in an influx of nutrients to urban spaces, in turn supporting greater abundance and predictability of resources, including greater prey availability (Sih et al. 2011; Fleming and Bateman 2018; Hansen et al. 2020). Species with flexible, diverse diets may be best placed to take advantage of increased resource availability in transformed landscapes (Newsome and van Eeden 2017; Fleming and Bateman 2018). Flexible carnivores may develop novel foraging strategies to exploit increased prey density, which can diminish search costs and reduce competition amongst predators (Berger 2007; Shannon et al. 2014; Fleming and Bateman 2018; Moll et al. 2018; Prugh and Sivy 2020; Sévêque et al. 2020). However, not all species are suited to urban ecosystems; the level of disturbance that can be beneficial to certain species can differ greatly (Nickel et al. 2020; Suraci et al. 2021). Trade-offs between risks and rewards are particularly common for mammalian carnivores, for which coexistence with humans is fraught (Oriol-Cotterill et al. 2015b; Blecha et al. 2018). In many instances, smaller predators stand to gain the most, as apex predators are invariably extirpated first (Ordiz et al. 2013; Oriol-Cotterill et al. 2015b), resulting in mesopredator release (Crooks and Soulé 1999; Prugh et al. 2009; Rebolo-Ifrán et al. 2017). Additionally,

smaller-bodied carnivore species have faster reproductive rates (Santini et al. 2019; Hill et al. 2020b) and are less likely to come into conflict with humans (Oriol-Cotterill et al. 2015b; Suraci et al. 2021) as they evoke less human fear responses than large carnivores (Clinchy et al. 2016; Ordiz et al. 2019; Suraci et al. 2019a). Moreover, smaller carnivores are more resilient to habitat loss as they have relatively fewer resource requirements and may therefore have higher likelihood of occurring in areas of high human influence (Evans et al. 2011; Aronson et al. 2016; Santini et al. 2019).

Behavioural responses to city life

Cities do not only act as filters, but they can shape evolution too. For those species not immediately extirpated, living in proximity to humans can exert strong selective pressures on heritable traits (Alberti et al. 2016, 2017; Fehlmann et al. 2020). Individuals with phenotypic traits or behavioural strategies that promote coexistence with humans are likely to persist more successfully in urban-dominated landscapes, and over time these traits will become more common in populations (Ordiz et al. 2011). In smaller, synanthropic species (i.e., species that live close to and benefit from humans; Guetté et al. 2017), being bolder and neophilic may be advantageous (Miranda et al. 2013; Canestrelli et al. 2016; Breck et al. 2019), e.g., bold individuals can take advantage of the rich food resources in cities (Arroyo et al. 2017). However, for those species that experience more frequent negative impacts with increased exposure to humans, such as larger carnivores (Ripple et al. 2014; Oriol-Cotterill et al. 2015b), shyer individuals are more likely to persist in transformed landscapes (Ordiz et al. 2019).

Spatial and temporal avoidance of humans and their activities are well-documented tactics used by wildlife in human-dominated landscapes (Gaynor et al. 2018, 2019). For instance, wildlife can avoid risks through temporal partitioning to reduce activity when humans are more active (Kronfeld-Schor and Dayan 2003; Péron et al. 2017) and a shift toward increased nocturnality in response to humans is commonly reported (Riley et al. 2003; Wang et al. 2015; Gaynor et al. 2018). For example, brown bears (*Ursus arctos*) in Sweden and Alaska avoid disturbed areas, especially during the day when human activity is high (Ordiz et al. 2014; Wheat and Wilmers 2016), while lions (*Panthera leo*) in Kenya forage closer to human structures at night (Suraci et al. 2019b). Medium-sized carnivores including bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) in the cities of Los Angeles (Riley et al. 2003) and Santa Cruz in the USA (Wang et al. 2015) increased their nocturnality to avoid human activity. However, avoidance strategies can be expensive, as wildlife expend more energy than may be optimal when mitigating non-starvation mortality risks (McNamara and Houston 1990; Houston et al. 1993). These behaviours can cause a reduction in the amount of time (Ordiz et al. 2012; Smith et al. 2015, 2017) or space (Wilmers et al. 2013) available for hunting and feeding, and promote costly (e.g., increased intense movement and less resting; Ordiz et al. 2014; Oriol-Cotterill et al. 2015a), inefficient (Nickel et al. 2021), or risky behaviours (Blecha et al. 2018). Eventually, the energetic consequences of living in a “landscape of fear” can translate to fitness effects which may influence population dynamics (Gallagher et

al. 2017; Blecha et al. 2018; Gaynor et al. 2019; Suraci et al. 2019a). Notably, changes in carnivore behaviour due to urbanisation may have disproportionate effects through cascading impacts on trophic webs (Hebblewhite et al. 2005; Oriol-Cotterill et al. 2015b; Kuijper et al. 2016). As urbanisation intensifies globally (McKinney 2002, 2006; Seto et al. 2012; Myers 2021), understanding the impact of changing land-use systems and elucidating the behavioural mechanisms that promote coexistence with carnivores is of considerable conservation value (Ripple et al. 2014; Van Cleave et al. 2018; Suraci et al. 2019b).

URBAN AREAS AS CLASSIC ECOLOGICAL TRAPS

Species select habitats which they associate with improved chances of survival and reproduction (Gilroy and Sutherland 2007). However, in areas of rapid and extensive environmental change, such as modern urban ecosystems, wildlife experience a slew of evolutionarily unfamiliar cues (Hale and Swearer 2016). Many risks in urban areas are not detectable to animals, such as increased disease or pollutant exposure (Bradley and Altizer 2007; Brearley et al. 2013; Murray et al. 2015). This mismatch between wildlife responses and risk cues associated with human disturbance can be problematic in two main ways (Smith et al. 2021). Either animals waste energy avoiding a benign stimulus (Type I error, false positive), or they fail to respond sufficiently to a lethal stimulus (Type II error, false negative; Lieber 1990). Where the mismatch in risk detection or assessment results in animals selecting habitats that were previously high quality (i.e., high prey availability) but are now associated with suboptimal conditions, such as increased probabilities of vehicle collisions (Mccardle and Fontenot 2016; Lamb et al. 2017), overexploitation (Van Der Meer et al. 2014; Pitman et al. 2015) or pollutant exposure (Ciach and Fröhlich 2013; Huang et al. 2018), this increase in Type II error can lead to an “ecological trap” (Robertson et al. 2013). These errors in judgement can scale up to influence individual fitness and ultimately shape population dynamics and ecological interactions (Remeš 2000; Penteriani et al. 2018; López-Perea et al. 2019; Smith et al. 2021).

Recently, there has been growing attention to “ecotoxicological traps”, where toxicant contamination risk is not correctly detected or assessed by animals in polluted human landscapes (Delibes et al. 2009; Huang et al. 2018; López-Perea and Mateo 2019; López-Perea et al. 2019). Environmental pollutants may be important drivers of traps as they pose health risks at an individual level that can be extrapolated to populations and further to ecological networks (Fernandez-de-Simon et al. 2018; López-Perea et al. 2019). This trap scenario has the potential to cause greater local and metapopulation consequences than those predicted by habitat degradation alone (Kristan 2003; Vonesh and Kraus 2009), ultimately contributing to species declines and local extinction in urban areas (Robertson et al. 2013; Penteriani et al. 2018). Although many species are impacted, carnivores may be particularly affected by urban ecotoxicological traps through their large habitat requirements and vulnerability to the bioaccumulation of toxicant due to their elevated

trophic positions (Riley et al. 2003; Bateman and Fleming 2012; Boyles and Nielsen 2017). Carnivores living within or adjacent to urban areas may therefore provide convincing evidence for ecotoxicological traps.

CARACAL ECOLOGY AND CONSERVATION

TAXONOMY AND EVOLUTIONARY CONTEXT

This study is focused on the caracal (*Caracal caracal*), a charismatic, medium-sized, solitary felid. It is recognisable by its large, black, tufted ears, a reddish coat with cream-coloured belly (hence the Afrikaans language name "rooikat" meaning "red cat"), short tail, and long hind limbs for leaping up to three metres to catch prey (Fig. 1.1). The caracal's elusive behaviour and camouflaged coat makes them difficult to detect in the wild. The species was first described as "*Felis caracal*" by J.C.D. von Schreber in 1776 from Table Mountain, Cape Town, in the Western Cape of South Africa (Pringle and Pringle 1979), where it still occurs. Recent analysis of DNA sequence data places the species into the genus *Caracal*, which contains both the caracal and the Vulnerable (VU; Bahaa-el-din et al. 2013), little-studied African golden cat (*C. aurata*; Johnson et al. 2006). Of the seven known small cat lineages, the clade containing caracals was the first to diverge from a shared common ancestor *c.* 8.5 million years ago (Ma; Janczewski et al. 1995; Pecon Slattery and O'Brien 1998). The serval (in the monospecific genus *Leptailurus*) then diverged *c.* 5.6 Ma, and the golden cat and caracal diverged *c.* 1.9 Ma (Johnson et al. 2006). While several sub-species were described through the 19th and 20th centuries, three main sub-species are currently recognized: the Southern caracal (*C.c. caracal*; Schreber 1776) from Southern and East Africa; the Northern caracal (*C. c. nubicus*; Fischer 1829) from North and West Africa; and the Asiatic caracal (*C. c. schmitzi*; Matschje 1912) that occurs in the Middle East through to India (Kitchener et al. 2017).

Fig. 1.1 Female caracal (TMC27 Disa) and kitten near Cape Point, Cape Peninsula, South Africa. Photograph by A. Adendorff (2015).

GEOGRAPHIC RANGE AND PREVIOUS LITERATURE

The caracal is widespread across much of sub-Saharan Africa, but it is also present through north Africa and the Middle East and through to northern India (Fig. 1.2A). Within South Africa the caracal occurs in a broad range of habitat types from peri-urban areas (i.e., areas immediately adjacent to a city or urban area; see Chapters 2 and 3) to the arid Karoo semi-desert, but is thought to prefer semi-arid woodlands, wetlands, grasslands and shrubland (Bothma 2012; Avenant et al. 2016).

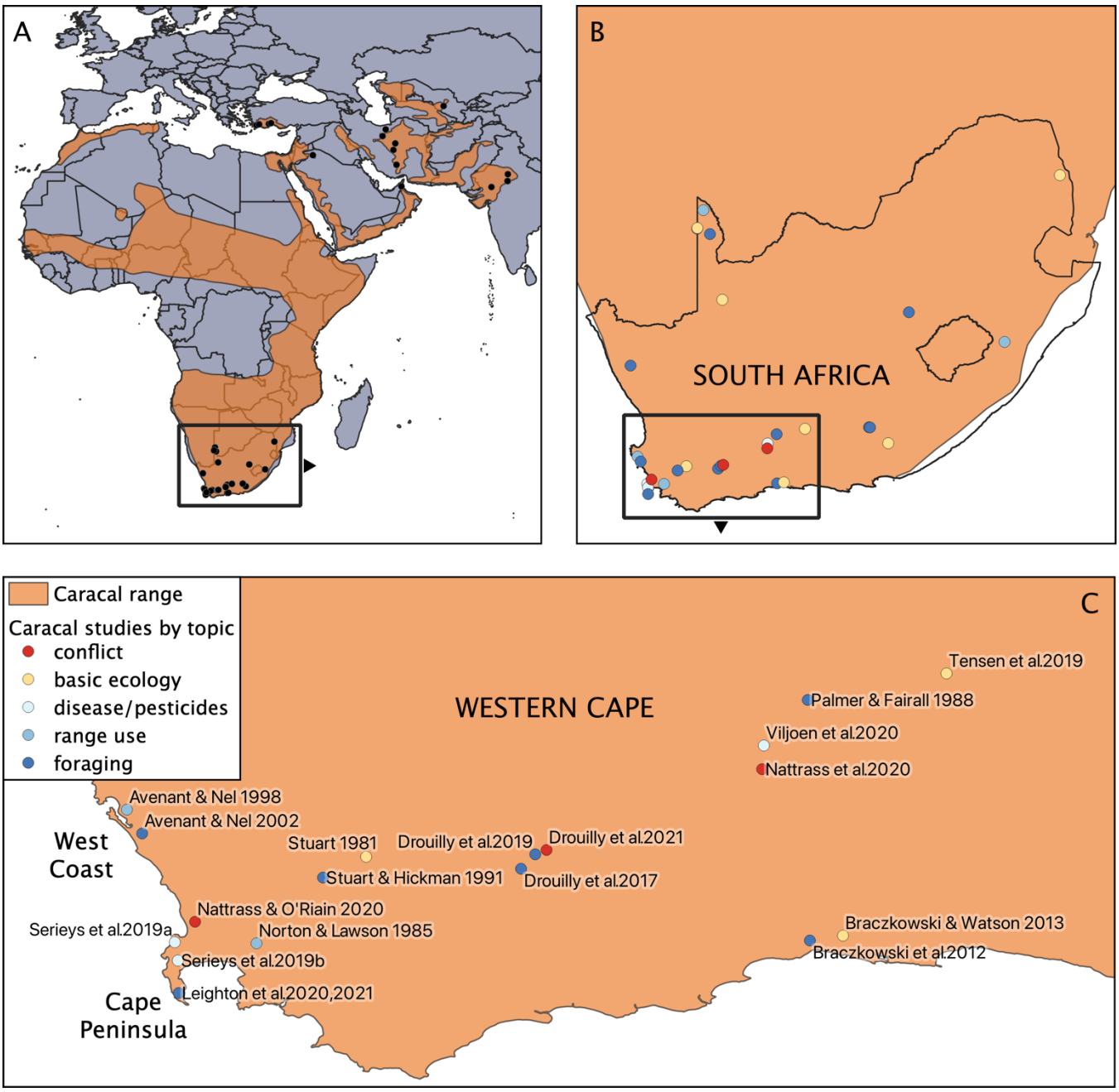


Fig. 1.2 Maps of **(A)** global caracal distribution (data from IUCN Red List, in orange) with approximate study site locations of 47 peer-reviewed, wild caracal-focused studies, with **(B)** studies in South Africa and **(C)** the Western Cape province coloured by topic.

Despite a cosmopolitan distribution, there is a dearth of studies on this medium-sized carnivore relative to sympatric big cats such as leopard (*Panthera pardus*) and lion (*P. leo*). South Africa is well represented in published research focusing on aspects of wild caracal ecology, with 30 studies in total, most falling within the Western Cape province (Fig. 1.2B). Research on caracals began in the 1970s, focusing on basic aspects of breeding and behaviour of captive individuals (Pringle and Pringle 1979; Bernard and Stuart 1987). The first published studies on the feeding habits of wild caracals emerged in the late 1970s and early 1980s in South Africa, but observational data had been collected prior to this (e.g., Bothma, 1965; Pienaar, 1969). Most studies in South Africa have focused on describing caracal diet in protected areas characterised

by natural vegetation (e.g., Pringle and Pringle 1979; Grobler 1981; Palmer and Fairall 1988; Avenant and Nel 2002) or on livestock farms where depredation was apparent (e.g., Moolman 1984; Stuart and Hickman 1991; Melville et al. 2004). Braczkowski et al. (2012) described caracal diet in two eastern coastal areas of South Africa (Fig. 1.2C) that have experienced considerable anthropogenic modification but there have been no studies to date focusing on caracal foraging ecology around rapidly expanding urban areas (but see Chapter 2; Leighton et al. 2020). There are also no studies focusing on wild caracals in their northern African range (i.e., north of South Africa), which incorporates at least 25 other countries (Fig. 1.2A). However, there are several published studies from the Middle East and Central Asia. These include observational studies in Saudi Arabia (Van Heezik and Seddon 1998), the United Arab Emirates (Stuart and Stuart 2007), Uzbekistan (Gritsina 2019), Iran (Farhadinia et al. 2007; Ghoddousi et al. 2009; Akbari et al. 2016; Moqanaki et al. 2016), Turkey (Giannatos et al. 2006; İlemin and Gürkan 2010; İlemin et al. 2020; Ünal et al. 2020), and northern India (Mukherjee et al. 2004; Singh et al. 2015; Khandal et al. 2020; Fig. 1.2A). This distribution and number of publications likely reflects their presence and relative densities in these countries. Density of caracals in South Africa is high and caracals are considered a problem animal by many farmers in the arid regions of southern Africa (Bothma 2012; Plessis et al. 2015; Drouilly et al. 2018). For example, Avenant & Nel (1998) found a density of 0.23 – 0.47 caracal/km^2 in the West Coast National Park, South Africa. As such, the IUCN Red List classifies the species as Least Concern (LC), but rare in the extreme north of their distribution, and as decreasing in north and west Africa (Avenant et al. 2016).

Behavioural and foraging ecology

While caracals are mainly nocturnal, they are also active during the day and demonstrate crepuscular peaks of activity. Males (~13 kg) are larger than females (~9 kg) and have larger home ranges. Where they have been studied, male home ranges vary between 27–280 km^2 and females between 7–40 km^2 depending on habitat and prey availability (Avenant and Nel 1998; Ramesh et al. 2017). In resource-limited, arid regions, such as the steppe desert of Saudi Arabia, a male caracal home range can be over 1,000 km^2 (Van Heezik and Seddon 1998), and in the Kalahari desert over 300 km^2 (Bothma and Le Riche 1994). By contrast, in mesic and productive habitats caracal home ranges can be as low as 8 km^2 (e.g., West Coast, Western Cape province, Avenant and Nel 1998; Drakensberg Midlands, Kwa-Zulu Natal province, Ramesh et al. 2017). Females can reproduce at 7–12 months and usually have 2–4 kittens after a 78–81 day gestation (Bernard and Stuart 1987). Subadult caracals stay with their mothers until ten months of age, after which they disperse, sometimes over 65 km from the natal site. In South Africa, due to few barriers to dispersal and a high tolerance to human disturbance, there is little evidence for caracal genetic spatial structuring across the country (Tensen et al. 2019).

Caracals have a notoriously catholic diet which contributes to their adaptability and widespread distribution, despite persecution and habitat modification. Caracals consume anything from insects to reptiles

and amphibians, but birds and small to medium-sized mammals form the bulk of their diet (Skinner and Chimimba 2005). In southern Africa, the caracal mainly preys on various species of grysbok (*Raphicerus spp.*), duiker (*Sylvicapra* and *Philantomba spp.*), small livestock (e.g., sheep and goats), vlei rats (*Otomys spp.*), rock hyrax (*Procavia capensis*), hare (*Lepus spp.*) and many species of birds (Pienaar 1969; Pringle and Pringle 1979; Grobler 1981; Palmer and Fairall 1988). Cannibalism has even been observed, with males eating kittens (Stuart 1981). Prey is mostly mammalian, but the importance of prey groups, such as rodent and ungulate, differs between studies. Stuart & Hickman (1991) found mammals from 15 g to 50 kg to be the most important prey category. On the West Coast of South Africa, where caracals have been relatively well studied (Fig. 1.2C), foraging rate varies with vegetation type and is positively correlated with the biomass of rodent prey (Avenant and Nel 2002). Similarly, a study in western India showed that rodents comprise a significant portion of the diet (Mukherjee et al. 2004). However, caracals are quintessential opportunistic generalists, feeding from a variety of sources, but tending to capitalise on the most available one (Avenant and Nel 2002).

Prey is generally stalked, and after a short rush, killed by a throat or nape bite. The carcass of a kill is usually consumed at the kill site, where feathers and thick fur are removed by incisors to access meat (Grobler 1981; Bothma 2012). Caracals may return to cached fresh prey. Stuart and Hickman (1991) speculate that caracals return to large kills to continue feeding only in areas where human persecution and the threat of predation by other predators are low. Much of the information currently available on caracal diet originates from stomach contents or scat analysis. The latter non-invasive method is preferable for elusive species, such as predators, that are difficult to observe and capture (Mukherjee et al. 1994; Foran et al. 1997). Detection of kills made by individuals using GPS collars or telemetry has only recently been published for caracals (e.g., Drouilly et al. 2019; Jansen et al. 2019; Leighton et al. 2020).

CARACALS IN A SOUTH AFRICAN CONTEXT

The caracal has a long history of negative interactions with people and livestock in South Africa. The species is ranked as one of the top nine in terms of human-felid conflict globally (Inskip and Zimmermann 2009), despite being relatively small. This may be attributed to their broader diet and distribution compared to similar-sized bobcats and lynx (*Lynx canadensis* and *L. pardinus*), allowing them to take larger ungulate prey, including livestock, over a larger spatial scale. In South Africa, small-livestock farmers are largely intolerant of caracals (Drouilly et al. 2021). Caracals are perceived as a severe threat to livelihoods (Drouilly et al. 2018) and damage-causing individuals can be legally hunted at any time of the year (Bothma 2012); although the efficacy of this predator control approach at reducing livestock depredation is unconvincing (Nattrass et al. 2020). Close to urban areas, such as Cape Town, conflict centres around domestic animals, where caracals are especially perceived as a threat to domestic cats (Nattrass and O'Riain 2020) despite low occurrence in their diet (see Chapter 2; Leighton et al. 2020). Caracals are also subject to both non-lethal and lethal management interventions in two coastal towns in the Western Cape of South Africa (Cape Town and

Betty's Bay) when predating on the two mainland colonies of the IUCN Endangered (EN) African penguin (*Spheniscus demersus*; BirdLife International 2020).

THE ECOLOGY OF CAPE TOWN

Cape Town is the oldest and second largest metropole in South Africa, with a long history of agriculture and development which intensified with colonial settlement starting in the mid 1600s (Anderson and O'Farrell 2012). The metropolis of the Greater Cape Town region isolates the dominant landscape feature of the city, i.e., the Cape Peninsula, from the mainland, thus creating an "island" with a strong north-south gradient of urbanisation (Fig. 1.3).

CLIMATE AND GEOLOGY

The Western Cape climate zone is Mediterranean with cool, wet winters (June – August) and warm, dry summers (November – February) in which fires are common. Rainfall varies dramatically across the Cape Peninsula, from over 1,000 mm to 350 mm per annum, and monthly average temperatures range between 25 °C for January and 17 °C for July (Mucina and Rutherford 2006). The dominant soils, derived from sandstone and shale, are low-nutrient and acidic (Cowling et al. 1996; Rebelo et al. 2011). The Cape Peninsula forms part of the Cape Fold Belt, an L-shaped band of mountains at the southwestern-most point of Africa, and therefore has high topological variation, from sea-level to 1,065 m at the top of Table Mountain with rockier, more montane areas in the northern portion of the Peninsula (Cowling et al. 1996). This geological variation combined with rivers, wetlands and coastal areas, results in a diversity of habitat types supporting a variety of plant and animal species and contributes to high landscape-level diversity (Goodness and Anderson 2013).

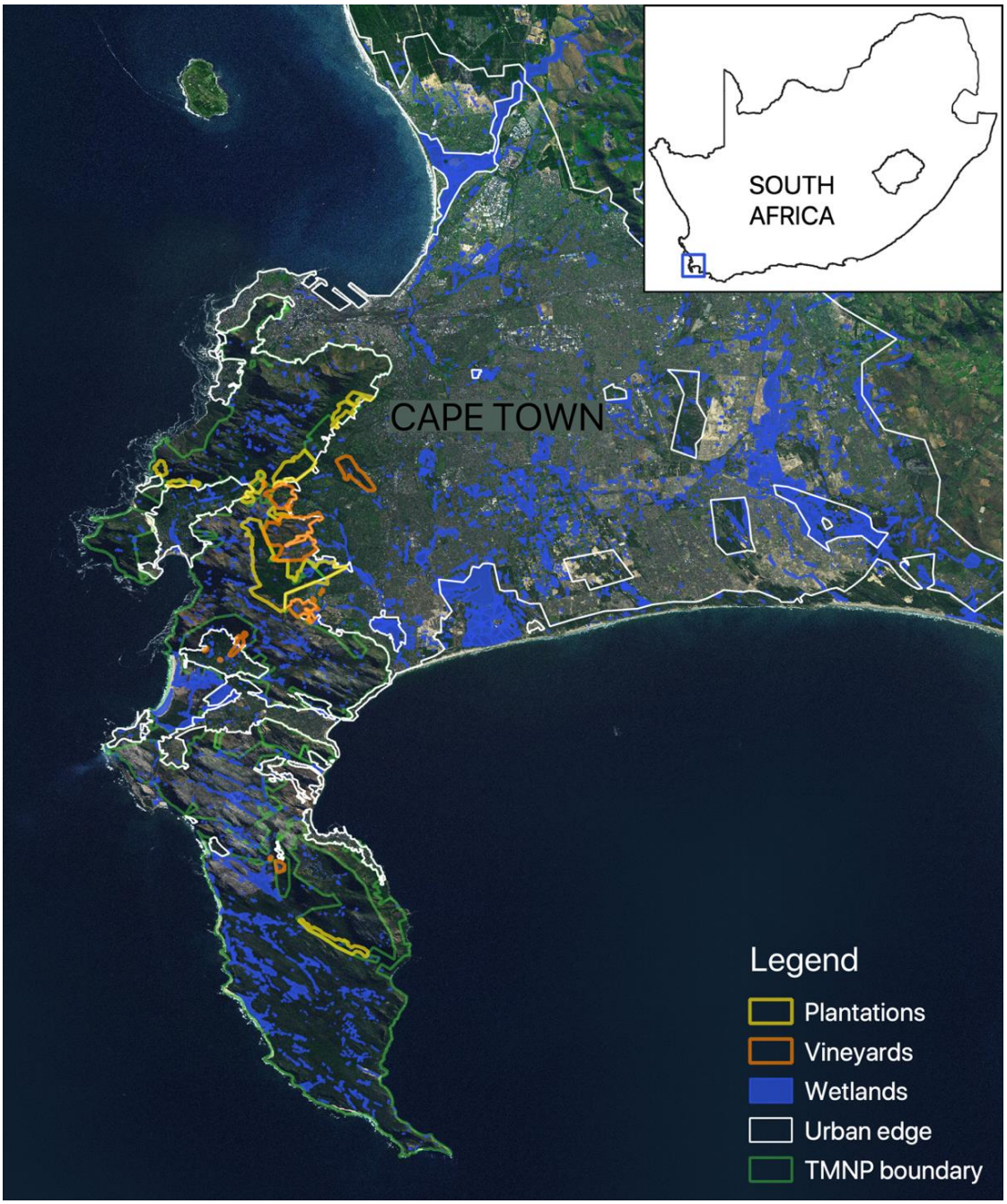


Fig. 1.3 Map of the Cape Peninsula study area (ESRI satellite imagery) showing the city of Cape Town urban edge (white line), pine and *Eucalyptus* plantations (yellow), vineyards (orange), wetlands and water bodies (blue) and the Table Mountain National Park (TMNP) boundary (green).

Biodiversity

The Peninsula falls within the Cape Floristic Region (CFR), a biodiversity hotspot, UNESCO World Heritage Site, and the smallest but most diverse of the six floral kingdoms globally (Myers et al. 2000). The remaining undeveloped, wildland habitat is mainly within the Table Mountain National Park (TMNP) which borders the city of Cape Town and the Atlantic Ocean (Fig. 1.3). The indigenous vegetation of Cape Town is comprised mainly of Mountain Fynbos (primarily Peninsula Sandstone Fynbos), Lowland Fynbos, Renosterveld, Strandveld, and a few pockets of Southern Afrotemperate forest (Mucina and Rutherford

2006). Fynbos is a fire-prone, fire-adapted, low–medium height shrubland which thrives in low-nutrient, sandy soils (Cowling et al. 1996; Mucina and Rutherford 2006). The number of indigenous plant species in Cape Town is estimated at 3,350, of which 190 are endemic to the Peninsula itself (Rebelo et al. 2011).

Along with extraordinary floral diversity, the Cape Peninsula has abundant and diverse fauna. While historically the area supported a number of now locally-extinct large- and medium-sized mammals including lion, leopard, jackal (*Lupulella mesomelas*), hyena (*Hyena brunnea* and *Crocuta crocuta*), African elephant (*Loxodonta africana*) and rhinoceros (*Diceros bicornis*), there are currently 74 mammal species thought to still occur within the Greater Cape Town region, 16 of which are endemic to South Africa (City of Cape Town Government 2018). The caracal is the largest remaining predator on the Cape Peninsula; the systematic removal of larger predators (e.g., lion, leopard and hyena) officially started in 1656 following the introduction of a bounty system by the then Dutch colonial administration (Skead 1980; Anderson and O'Farrell 2012). The Cape lion (*Panthera leo melanochaita*) was fully extirpated by the 1850s, while the last leopard (*Panthera pardus pardus*) was reportedly sighted on the Peninsula in the 1930s. Leopards are still present in the Limietberg and Boland mountains to the north and east of the Greater Cape Town area, respectively. Co-occurring mammalian carnivores on the Peninsula include the Cape grey mongoose (*Galerella pulverulenta*), water mongoose (*Atilax paludinosus*), large spotted genet (*Genetta tigrina*) and Cape clawless otter (*Aonyx capensis*). Other mammals include the rock hyrax, a medium-sized afrotherian inhabiting cliffs and rocky outcrops, Chacma baboons (*Papio ursinus*), as well as numerous small mammals (e.g., golden moles and shrews) and rodents (e.g., mole-rats, four-striped grass mice, *Rhabdomys pumilio*, and vlei rats, *Otomys irroratus*).

There are currently 374 recorded bird species in the Cape Town area, 16 of which are endemic to South Africa and six of which are endemic to the CFR (City of Cape Town Government 2018). Many species are synanthropic and abundant in the transformed areas of Cape Town (Suri et al. 2017). Helmeted Guinea fowl (*Numidia meleagris*), Egyptian geese (*Alopochen aegyptiaca*), and several species of ibises, pigeons and doves are common in vineyards, golf courses, school grounds and suburban gardens. Additionally, there are an estimated 65 reptile species within the city and its surrounds, 30 of which are endemic to South Africa, and 27 amphibian species within the city boundaries, two of which are endemic to the CFR (City of Cape Town Government 2018).

Human influences and development

The developed areas of the Greater Cape Town region form a complex mosaic of urban, residential, industrial, greenbelt, and agricultural areas intersected by an extensive road and railway network. On the Peninsula, viticulture and forestry date back to the early 1650s and vineyards are the main form of agriculture today, along with commercial pine and *Eucalyptus* plantations (Anderson and O'Farrell 2012; Fig. 1.3). The

urban area of Cape Town increased significantly after the turn of the 20th century, trebling between 1946 and 1977, and then doubling again by 2002 (Sinclair-Smith 2009; Rebelo et al. 2011). Ongoing habitat loss due to the urbanisation of the Greater Cape Town region continues to jeopardise both local ecosystems and endemic animals and plant species. A recent study by Schnetler et al. (2020) confirmed the presence of only 19 medium to large mammal species across most of Cape Town's nature reserves in contrast to the 39 predicted to be in the region. Of the plants, 300 are now threatened and 13 are extinct in the wild (Rebelo et al. 2011) with the greatest losses occurring in the lowland areas as a result of urban development and agriculture (Holmes et al. 2012). Biodiversity is also affected by the anthropogenic changes in the species community on the Peninsula. As in other port cities, Cape Town has many naturalised alien species across diverse taxonomic groups, including over 450 plant and 38 animal species (Holmes et al. 2012). Introduced plants, especially Australian wattles (*Acacia spp.*), have degraded vast areas of the unique CFR vegetation types (Holmes et al. 2012). Introduced animal species, with varying ecological effects on native species, are commonly found in Cape Town's suburbs and green spaces, including grey squirrels (*Sciurus carolinensis*), brown rats (*Rattus norvegicus*), house mice (*Mus musculus*), and livestock including sheep, goats, peacocks, chickens, and geese. Additionally, biodiversity is threatened by an increase in anthropogenic fires, which occur at higher than natural rates and intensity (Forsyth and Van Wilgen 2008).

The City of Cape Town's human population is expected to expand rapidly, from 4.1 million people in 2015 to 5.5 million in 2030 (Western Cape Government 2017; United Nations 2019). This growth has led to an increase in demand for housing accompanied by the expansion of informal housing settlements (Housing Development Agency 2012; Turok and Borel-Saladin 2014; City of Cape Town Government 2021), further threatening undeveloped areas and placing extensive strain on service delivery (Holmes et al. 2012; Pan et al. 2015). Waste management is a major issue in the city; Cape Town has struggled with poor water sanitation and air quality since the 1800s (Anderson and O'Farrell 2012). Ongoing organic and inorganic pollution and littering of Cape Town's terrestrial, freshwater and marine systems pose a threat to both wildlife and human health. This includes illegal dumping of industrial chemicals, run-off from agricultural activities and sewage spills (City of Cape Town Government 2018). There is increasing evidence that various toxic environmental pollutants spill over into agricultural and industrial soils (Ayeni et al. 2010; Malan et al. 2015) and natural forest patches (Krüger et al. 2019), and bioaccumulate in local predators, such as the Near Threatened (NT) Cape clawless otters (Jacques et al. 2015; Okes 2017), the Endangered (EN) Black harrier, (*Circus maurus;* BirdLife International 2017; Garcia-Heras et al. 2018), and caracals (Serieys et al. 2019; see Chapter 4).

BROAD STUDY AIMS AND OBJECTIVES

The aim of this study is to investigate how urbanisation influences the foraging ecology and ecotoxicology of a medium-sized carnivore, the caracal, using a mosaic of land-use types within and adjacent to the Cape Town metropolis. The objectives include (i) assessing the contribution of human-associated prey through comprehensive estimates of diet composition, (ii) quantifying the degree of resource selection across the Peninsula and the influence of human disturbance on feeding behaviour, and (iii) evaluating the potential ecotoxicological threat and health impacts of environmental pollutants. Together these results allow for an assessment of risk-reward trade-offs for caracals that exploit or avoid human transformed landscapes, and directly inform our understanding of the broader implications for the city's wildlife at a time of increasing urbanisation.

THESIS OUTLINE

This thesis is presented as a series of stand-alone chapters formatted to facilitate publication (Chapters 2–4).

In **Chapter 2**, I integrate scat and GPS cluster methods to inform a detailed dietary analysis for caracals along the urban gradient of the Cape Peninsula. The main findings of this chapter have been published in *Urban Ecosystems* (DOI: 10.1007/s11252-020-00946-y).

In **Chapter 3**, I quantify the influence of urbanisation on spatial foraging resource selection, compare three dietary datasets and investigate caracal behavioural strategies that promote coexistence at the urban edge. I present and implement the first use of the integrated-diet method for resource selection analysis. The main findings of this chapter have been published in *Animal Conservation* (DOI: 10.1111/acv.12732).

In **Chapter 4**, using samples collected from both GPS monitored individuals and opportunistically collected mortalities I quantify caracal exposure to several toxic environmental pollutants, and assess possible sources of exposure and potential physiological impacts.

In **Chapter 5**, I summarise and contextualise my key findings within the framework of how best to mitigate the risks to caracal from a range of threats to which they are exposed on the Peninsula. Here the goal is to propose interventions that are likely to reduce their exposure to environmental pollutants, vehicle collisions and negative interactions with people and their pets.

ETHICS STATEMENT

All animal capture, handling, and sampling followed ethical guidelines approved by the American Society of Mammologists, the University of Cape Town Animal Ethics Committee (2014/V20/LS), Cape Nature (AAA007-0147-0056), and South African National Parks (SERL/AGR/017–2014/V1).

CHAPTER 2

AN INTEGRATED DIETARY ASSESSMENT INCREASES FEEDING EVENT DETECTION IN CAPE TOWN'S CARACAL POPULATION

A version of this chapter has been published as:

Leighton, G.R.M., Bishop, J.M., O'Riain, M.J., Broadfield, J., Meröndun, J., Avery, G., Avery, D.M. & Serieys, L.E.K. (2020) An integrated dietary assessment increases feeding event detection in an urban carnivore. *Urban Ecosystems* 23, 569–583. https://doi.org/10.1007/s11252-020-00946-y

ABSTRACT

Urbanisation radically changes habitats and alters available resources. Populations of large, highly mobile species are often extirpated at the urban-wildland interface, while medium-sized carnivores may thrive through reduced predation and competition for prey. I investigated the diet of the caracal (*Caracal caracal*), a medium-sized felid inhabiting patchy natural habitat isolated within and adjacent to the dense urban matrix of South Africa's second largest city, Cape Town. To obtain comprehensive dietary estimates, I integrated two classic dietary methods, scat and GPS cluster analysis, by accounting for gut transit times. As part of a larger movement ecology study, 26 individuals were GPS-collared over a two-year period (2014 – 2016) to generate coarse (3-hour) and fine-scale (20-minute) GPS movement data. Using the movement data, 677 GPS-clusters were identified and investigated for prey remains. Over 650 scats were collected, half of which were found at GPS-clusters and were linked with the individual sampled. By systematically correcting for a range of gut transit times, I determined whether scat at cluster sites was from the same or an earlier feeding event, thereby increasing the overall detection of feeding events by > 50%. Avian species dominated GPS clusters with prey remains while micromammals were overwhelmingly represented in scat. Although > 40% of feeding events occurred within 200 m of the urban edge, caracals largely preyed on native, wild species. My findings contribute to our understanding of how diet flexibility can contribute to species persistence in sub-optimal conditions where they face multiple novel stressors. Further, this integrated-diet approach could be incorporated into studies that estimate foraging-explicit resource selection and habitat preference, where it can provide a more nuanced understanding of foraging habitat use for carnivores feeding on a range of prey sizes.

INTRODUCTION

Urbanisation leads to widespread alterations in available resources through drastic habitat modification, affecting certain species disproportionately (McKinney 2002; Shochat et al. 2006). Populations of highly mobile carnivores with large resource requirements are often the first to be extirpated due to habitat loss and fragmentation (Crooks 2002; Ordeñana et al. 2010; Lowry et al. 2013). In contrast, generalist mesocarnivores (defined as medium-sized predators with body mass < 34 kg and an average of 13 – 16 kg, Roemer et al. 2009; Wallach et al. 2015) may find more abundant smaller prey in urban and peri-urban areas, through bolstered populations of native or introduced species (Roth and Lima 2003; Moss et al. 2016; Smith et al. 2016; Hansen et al. 2020) and thus thrive (Chace and Walsh 2006; Prugh et al. 2009; Bateman and Fleming 2012). However, exposure to human activities and novel species in and around urban areas presents the risks of a spillover of pathogens and the bioaccumulation of pesticides (Bradley and Altizer 2007; Riley et al. 2007; Serieys et al.

2019). Understanding the extent to which medium-sized carnivores are able to exploit human-derived food resources at the urban edge, and whether this facilitates their ability to persist in human modified landscapes, is critical to mitigate threats, alleviate human-wildlife conflicts, and promote biodiversity conservation globally at a time when natural areas are increasingly lost to and transformed by urbanisation (Bateman and Fleming 2012; Allen et al. 2016; McPherson et al. 2016). Mesocarnivores are thus potentially valuable sentinels of ecosystem health in human modified landscapes (Jooste et al. 2013).

Knowledge of the diet of free-ranging species is pivotal to understanding their ecology (Litvaitis 2000). For wild carnivores, a single unified approach to diet studies is not established, likely due to highly variable species and study systems and the multitude of techniques available (Litvaitis 2000; Bacon et al. 2011; Klare et al. 2011). Our understanding of the fundamental ecology of populations may therefore be biased by imperfect methodologies that do not provide comparable information (Litvaitis 2000; Klare et al. 2011; Morin et al. 2019). While there are many options available for dietary analysis, such as DNA metabarcoding (Shehzad et al. 2012; De Barba et al. 2014) and stable isotopes (DeNiro and Epstein 1978; Newsome et al. 2015a), an overwhelming number of carnivore diet studies rely on scat (Klare et al. 2011). Scat analysis is often preferred because samples can be relatively cheaply, easily and non-invasively obtained on the landscape, whereafter undigested prey remains can be used to determine prey biomass and relative frequency in the diet (Klare et al. 2011). An inherent bias to this approach, however, is that small prey consumed in their entirety (i.e., including all bones and hair) will be overestimated. Conversely, large prey that have lower surface area-to-volume ratio have less indigestible matter per unit biomass, leaving little evidence in scat. The result is a diet assessment overrepresented by small prey species (Lockie 1959; Floyd et al. 1978; Marker et al. 2003).

An alternative, commonly used, approach for carnivores relies on locating unconsumed prey remains from individual feeding events. Data collected via GPS-enabled collars can be mapped to locate clusters of GPS-points on the landscape ("GPS clusters") which can form when an animal is feeding or at rest (Anderson and Lindzey 2003; Sand et al. 2005; Martins et al. 2011; Kindschuh et al. 2016). The GPS cluster approach is traditionally used for predators that consume large prey with long handling times (e.g., deer and elk, Anderson and Lindzey 2003; Knopff et al. 2009). The approach has been used on large predators that consume relatively smaller prey (e.g., mountain lions, *Puma concolor*, predating domestic cats, Smith et al. 2016). However, using GPS clusters is impractical to detect micromammal or invertebrate prey that have very short handling times. Consequently, carnivore diet studies that rely on GPS clusters vastly underrepresent small prey (Bacon et al. 2011; Pitman et al. 2014).

For medium-sized carnivores that predominantly prey on smaller species, GPS clusters may not form with the longer fix rates traditionally used. Even if GPS clusters do form, few prey remains may be left behind. The potential to discover remains of small prey is thus often assumed to be unfeasible (e.g., prey 5 – 10 kg, Bacon et al. 2011; Elbroch et al. 2017; Knopff et al. 2009) and hence is seldom explored by mesocarnivore

ecologists.

Here I first use two classical approaches, scat and GPS-cluster analysis, to characterise the diet of a common medium-sized felid, the caracal (*Caracal caracal*, Skinner and Chimimba 2005), living adjacent to one of South Africa's most rapidly urbanising cities, Cape Town (Turok and Borel-Saladin 2014). Previous studies in protected natural and agricultural areas report that caracal prey opportunistically on a diverse range of species, typically within the 0.5 – 10 kg size range (e.g., Grobler 1981; Avenant and Nel 1998, 2002; Drouilly et al. 2019; Jansen et al. 2019). Next, with an understanding of the inherent biases of the GPS-cluster towards detecting large-prey (Knopff et al. 2009), and the scat approach towards detecting micro-mammal prey (Klare et al. 2011), I describe a third approach that refines our understanding of caracal diet in transformed landscapes. Specifically, I integrate the findings of the GPS-cluster and scat-based approaches by controlling for gut transit times and, in doing so, systematically verify and incorporate missed feeding events undetected with each approach independently (Marucco et al. 2008; Tambling et al. 2012; Pitman et al. 2014). Integrating scat and GPS cluster data while correcting for gut transit times to remove duplicate feeding events (see Methods, Fig. 2.2) may provide a more complete understanding of diet, particularly in medium-sized generalist carnivores where prey size range may vary considerably (Svoboda et al. 2013; Kays et al. 2015; Vogt et al. 2018). I then describe and quantify prey species detected using the two classical approaches. Additionally, I assess the relative proportion of wild indigenous, synanthropic, and exotic prey (see Methods section 6) across the three approaches. I also compare prey detection efficacy using fine-scale (20-minute GPS intervals) and coarse (three-hour interval) GPS-collar sampling frequency, with the expectation that fine scale data would allow for more smaller prey remains to be detected. Finally, because the majority of GPS-clusters and scat were found within 500 m of the urban edge, exotic and synanthropic species associated with urban areas are expected to dominate caracal diet in the study area (Bateman and Fleming 2012). Understanding and accurately describing the diet of adaptable medium-sized carnivores is important in urbanising areas where conflict with humans and their pets is commonplace (Bateman and Fleming 2012; Soulsbury and White 2015) and predators are vulnerable to bioaccumulation of toxicants through their prey (Serieys et al. 2015, 2019; Boyles and Nielsen 2017; Rodríguez-Estival and Mateo 2019).

METHODS

STUDY AREA

Caracal diet was investigated in the Cape Peninsula (hereafter "Peninsula"), a highly fragmented mosaic of urban, rural and natural land within the Cape Floristic Region, a biodiversity hotspot recognised as one of the most threatened ecosystems and a global priority for conservation (Underwood et al. 2009). The Peninsula comprises approximately 300 km^2 of wildland (i.e., predominantly indigenous vegetation including

formally protected areas and undeveloped land), falling mostly within the Table Mountain National Park (TMNP) and adjacent to the urban metropolis of Cape Town (Fig. 2.1). The national park is fragmented by a variety of human land uses including residential and agricultural areas, light industry, roads, and altered-open areas, such as golf courses and manicured school grounds. Potential prey species in the study area included exotic species (e.g., introduced brown rat, *Rattus norvegicus,* Eastern grey squirrel, *Sciurus carolinensis,* and pets and livestock), indigenous synanthropic species (e.g., Egyptian goose, *Alopochen aegyptiaca*, Helmeted Guinea fowl, *Numida meleagris,* and Hadeda ibis, *Bostrychia hagedash*), and > 530 indigenous wild species (Rebelo et al. 2011).

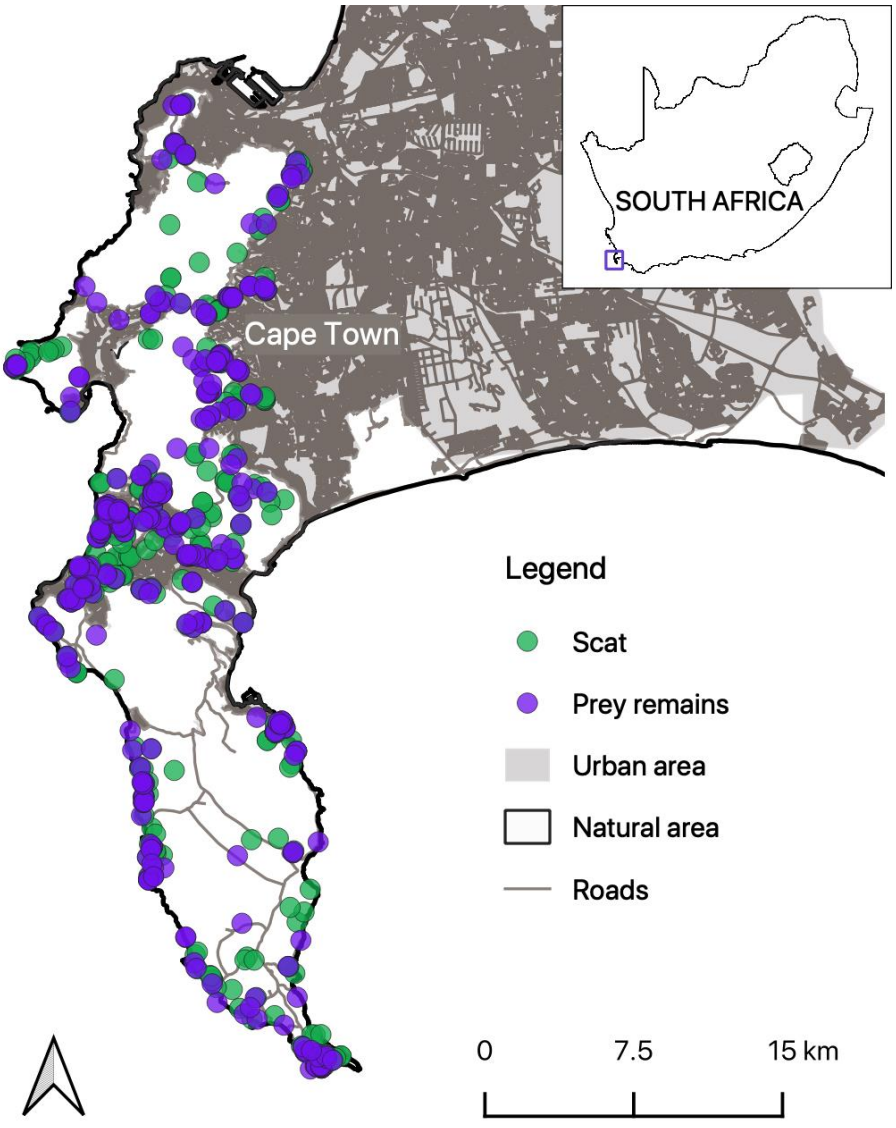


Fig. 2.1 Map of the Cape Peninsula study area in South Africa showing the locations of caracal prey remains (n = 385) and scats (n = 654) found opportunistically and at GPS clusters and analysed in this study.

Capture and GPS-collaring

Twenty-six caracals were captured and GPS-collared between 2014 – 2016 using standardised cage-trapping techniques. Briefly, custom built mesh wire cage traps or Tru–catch traps (Bell Fourche, South Dakota) were baited with a variety of visual, audio, and scent lures. Traps were checked a minimum of every

8-hours. Once captured, individuals were immobilised using 7 mg/kg ketamine HCl and 0.08 mg/kg medetomidine HCl. Age class, sex, weight, and morphological measurements were recorded. Individuals were classified as subadults (< 2 years) or adults (≥ 2 years) based on body size, weight, tooth wear and eruption, and reproductive status (Schroeder et al. 2005). A variety of samples were collected at captures (blood, hair, etc.), including faecal samples (n = 12).

Individuals were fitted with GPS-collars (FollowIt™ Tellus, Lindesberg, Sweden) equipped with a drop-off mechanism that activated within six months of collar fitting. All collars were also fitted with a rot-off cotton spacer to ensure eventual drop-off. As part of a larger caracal movement ecology study, collars were programmed to collect GPS locations at two fix intervals: i) coarse scale: every three hours throughout the 24-hour cycle resulting in eight locations per day, and ii) fine scale: on every 9 – 10th day, 20-minute fixes were collected for 24 – 36 hours resulting in up to 108 consecutive 20-minute GPS locations per day. Finally, caracal carcasses were opportunistically collected and necropsied, from which faecal samples were recovered (n = 3).

GPS CLUSTER IDENTIFICATION AND SEARCH PROTOCOL

The GPS data were downloaded weekly using the FollowIt™ GEO web interface. I used a rule-based Python algorithm (Python Software Foundation) to identify GPS clusters following Knopff et al. (2009). The algorithm defined clusters as ≥ 2 GPS locations within a 100 m distance of each other within a 24-hour interval. To compare the effect of fix rate on prey size detected I used both three-hour and 20-minute fix intervals to identify clusters. I prioritised clusters using a set of decision rules implemented in Python that ranked each cluster as follows: a cluster ranked higher if it had i) a smaller cluster radius (< 50 m), ii) a time span of > 3 hours, iii) a cluster fix success of over 75%, and iv) high site fidelity (i.e., the ratio of points spent away from the cluster/actual number of points in that time period was < 25%). I used the same rule-based algorithm on all the data, so clusters formed during the 20-minute fix schedule were ranked lower because there would be more GPS locations in closer proximity recorded for the same time period. The centroid, time elapsed, radius, number of points away from the cluster and fix success rate were generated and recorded for all clusters.

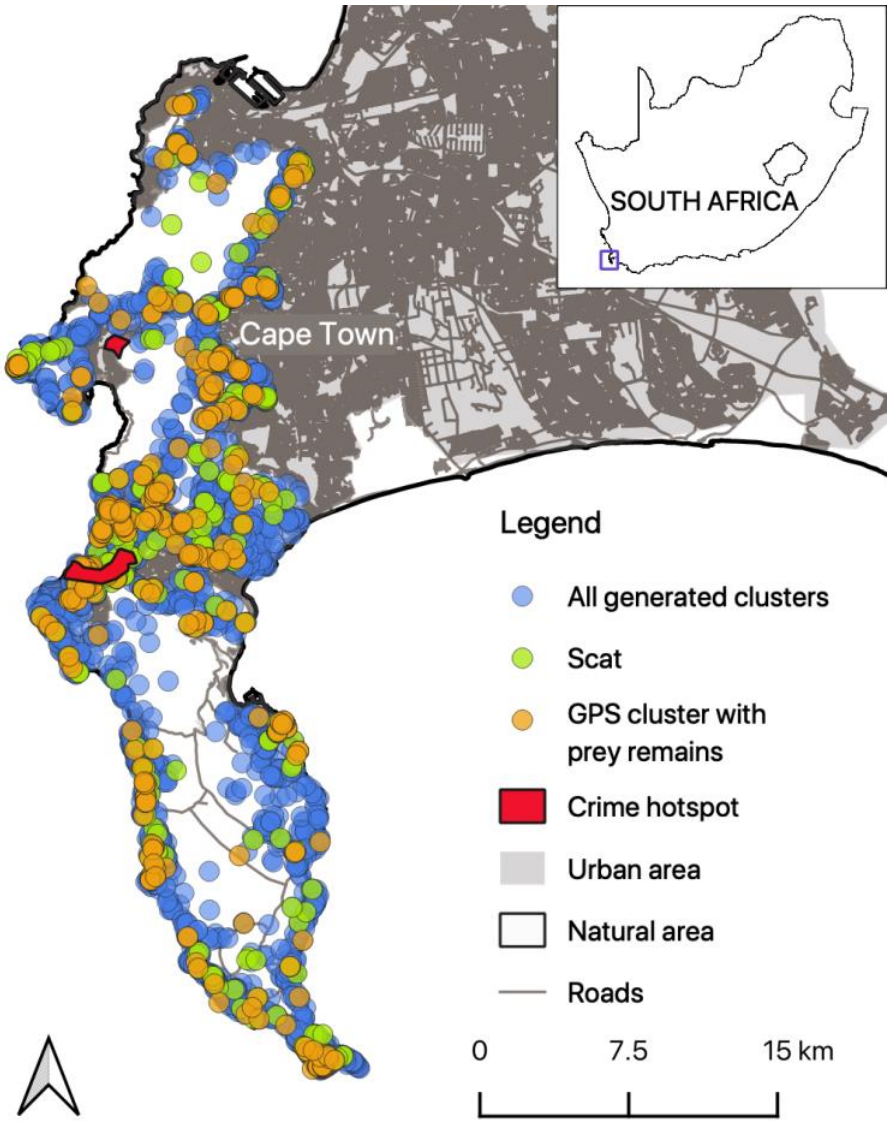


Fig. 2.2 Map of the Cape Peninsula study area in South Africa showing the locations of all generated caracal GPS clusters (blue, n = 4202), GPS clusters with prey remains (orange, n = 385), scats (green, n = 648) and the two crime hotspots (red) avoided during fieldwork investigations. These areas were visited on occasion when accompanied by armed guards from SANParks.

The study presented logistical constraints that limited the ability to visit every GPS cluster. First, far more clusters were identified than could feasibly be investigated. Second, field visitations were spatially restricted to areas that were considered safe (by local South Africa National Parks, SANParks, liaison officers) from violent crime. There were two small (< 3km^2) urban crime hotspots adjacent to lower socio-economic status areas that were unsafe to visit without armed guards (see Fig. 2.2). While it is possible that avoiding these two unsafe areas may have biased the diet results, these areas were not ecologically distinctive and both habitat types were sampled extensively in other areas, as well as directly adjacent to these sites. Field visitations were coordinated to access multiple clusters near each other. The centroid of the selected clusters was found within an average of 16 ± 10 SD days and a standardised search protocol was followed. Briefly, a 50 m radius around the cluster centroid was searched for a minimum of two hours, as has been used for

ecologically similar species (Svoboda et al. 2013 bobcat, *Lynx rufus*; Podgorski et al. 2008 Eurasian lynx, *Lynx lynx*). The area was searched for prey remains (i.e., carcass, hair, feathers, etc.), scat, resting beds (i.e., site with evidence of caracal resting), and scratching posts. Prey remains were photographed *in situ* and collected. I later identified the remains macroscopically using reference feathers and species guides (Hockey et al. 2005), hair samples, and taxidermic specimens housed at the University of Cape Town.

SCAT COLLECTION AND ANALYSIS

Caracal scats were identified by their unmistakable size, shape, and visible content (Skinner and Chimimba 2005). The chance of misidentification was low because there are no other medium-sized canid or felid predators in the study area. Despite extensive fieldwork effort, scats were rarely detected except during cluster investigations. A small section of the scat was left where it was found in the field in case it was an important mode of communication between individuals in the study area (Stuart 1981). Upon collection, scats were visually grouped into categories (fresh, old, and decomposed) based on visual characteristics (colour, dryness, etc.) and level of degradation. For those samples that plausibly matched the age of the cluster, I classified the scat as produced by that caracal at the start of the cluster formation. Those samples found at the clusters (i.e., within the 50 m radius) that were too old or too fresh to belong to that cluster based on cluster duration and time to cluster investigation were classified as opportunistic. Scats were also classified as opportunistic if they were: i) collected in the field but not associated with clusters (i.e., outside of the 50 m radius), ii) were collected during captures (n = 12), or iii) collected during necropsies (n = 3).

Single scats were placed in pieces of nylon stocking tied at both ends with colour-coded elastic bands and soaked in warm water with liquid wool laundry detergent (Woolite®, approx. 100 – 120 mL to 5 L water) for approximately 24 hours. The stockings were then cut open and the contents washed by hand under running water in a metal sieve (mesh size of 1 mm) to remove unidentifiable micro-fraction. The remains were placed in a petri dish, separated into prey type and the percentage composition of each prey (up to three groups) was estimated. Petri dishes were placed in a drying oven at 30 – 40°C and dried overnight. The dried contents were then sorted, separating out the hard matter (bones, teeth, hooves, nails, and claws) from the hair and vegetation and placed into labelled bags for later inspection.

A combination of methods was then used to identify the prey remains (Norton et al., 1986). The bones of birds and larger mammals were classified to the finest taxonomic level using osteological reference material at the Iziko South African Museum with the assistance of G. Avery. Rodent postcranial bones were compared to reference material at the Iziko South African Museum and Monadjem et al. (2015) with the assistance of D.M. Avery. I counted the number of prey individuals in scats found in the same cluster using left and right bones (e.g., limb bones, clavicles, mandibles, and coracoids) when possible. Using the hair impression methods described by Ott et al. (2007), I examined the microscopic characteristics of hair for the

remaining samples. Reptile remains (e.g., scales) and insect fragments were identified to genus or family level where possible. To minimise pseudo-replication, scat samples collected in close proximity on the same day (i.e., in the same cluster) and containing the same prey species were combined (Tambling et al., 2012; Perilli et al., 2016), except where more than one individual prey item was identified using left and right bones.

Integrating scat and GPS cluster-located prey remains findings with gut transit times

Each prey item identified from a scat found at a GPS cluster was classified as: i) consistent with the prey identified from prey remains at that cluster, ii) consistent with the prey identified at the previous cluster, or iii) inconsistent with prey identified at either that cluster or the previous cluster (i.e., a missed feeding event; summarised in Fig. 2.3). I then used gut transit times, as in Tambling et al. (2012) and Pitman et al. (2014), to further refine my classifications above. Two extreme gut transit times were set, a minimum of 0.5 days and a maximum of 4 days for caracals, based on similar-sized jungle cat (*Felis chaus*) feeding trial digestion rates (12 – 84 hours, Chakrabarti et al., 2016). The minimum and maximum gut transit times correspond to a high and low level of bias in terms of missed feeding events (Tambling et al. 2012).

Scats produced at GPS clusters and within the gut transit widow of a caracal are expected to contain the remains of the species found at that cluster or at previous clusters for that caracal individual within the gut transit time limit (Fig. 2.3). Scat samples found outside of the gut transit times and/or consisting of species other than the prey remains found at the cluster were considered missed feeding events. If a cluster had the same species in the scat and the prey remains but the cluster time span was < 12 hours, then I classified it as a missed feeding event, as the prey could not have been digested within the assigned gut transmit limit. Similarly, if the cluster was formed over > 12 hours, then the scat was classified as corresponding to that cluster (i.e., a duplicate record of a feeding event). If the cluster scat prey item was the same species as the prey remains at both current and previous clusters, then the age category of the scat was used to decide to which cluster it belonged. The integrated scat and GPS cluster-located prey remains databases ("integrated-diet" approach) therefore contained all prey remains found at GPS clusters together with the missed feeding events identified from the scats found at GPS clusters at 0.5-day and 4-day gut transit limits. The duplicate feeding events (i.e., those prey items in scat that were the product of prey remains at the cluster or a previous cluster) were discarded.

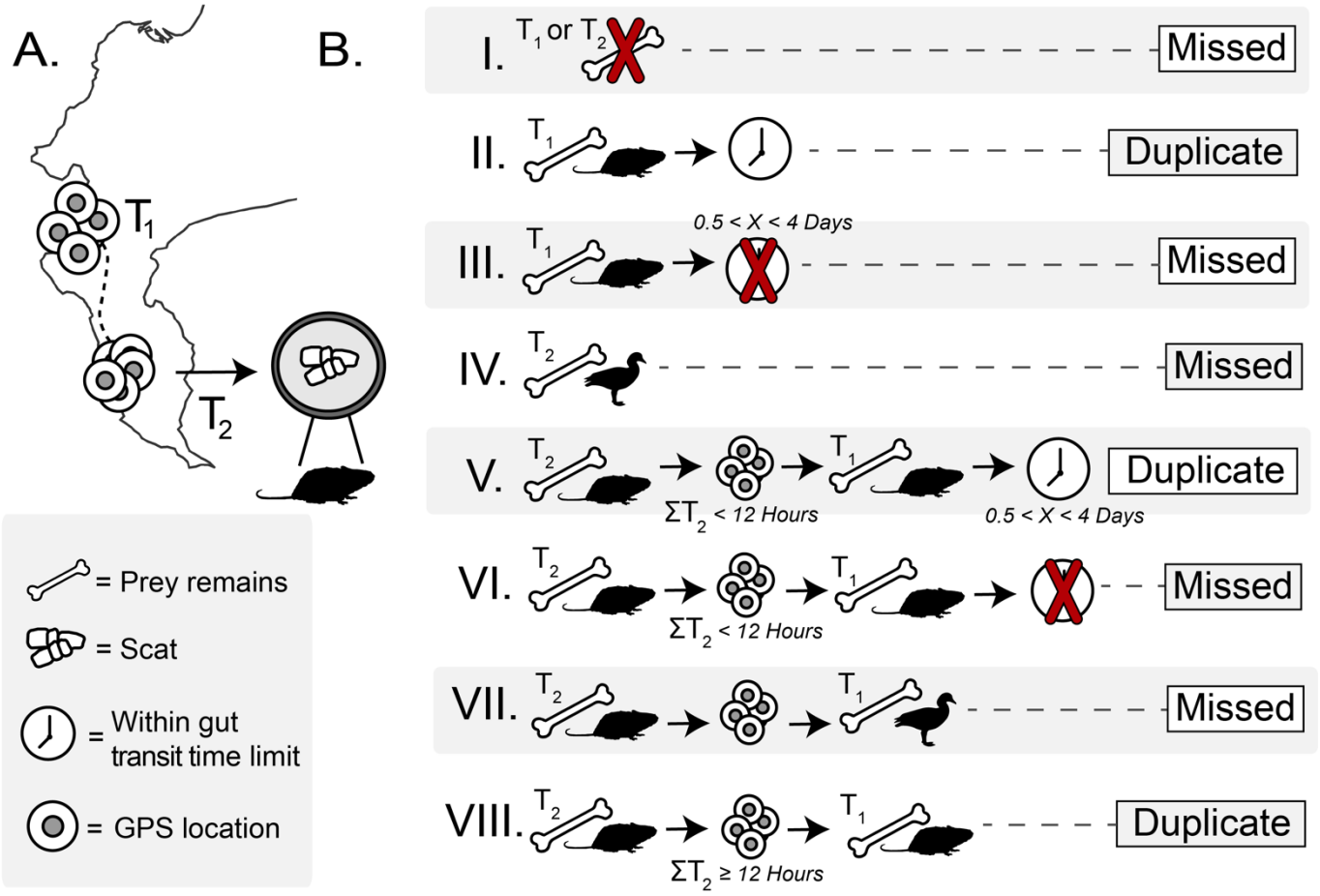


Fig. 2.3 Concept diagram used to classify prey items found in scats found at clusters as i) a duplicate feeding event (either the product of prey remains at that cluster, or the product of prey remains at a previous cluster), or ii) a missed feeding event (i.e., a product of prey undetected by GPS cluster analysis).

(**A**) Two hypothetical, chronological clusters in the study area generated by the same individual caracal. A scat is found at a GPS cluster (T_2).

(**B**) The scat contains a prey item. If there were no prey remains at cluster T_1 or T_2 then this represents a missed feeding event (**I**). If prey remains are present at the previous cluster T_1 and they are from the same species as the scat prey item and within the gut transit time limit (i.e., 0.5 or 4-day) then it is a duplicate feeding event (**II**). If prey remains are present at the previous cluster T_1 and it is the same species as the scat prey item, but it is outside the gut transit time limit, the prey item could not have been digested in time and it represents a missed feeding event (**III**). If prey remains are present at T_2 and are from a different species from the scat prey item, then the scat prey item is a missed feeding event (**IV**). If there are prey remains present at T_2, they are the same species as the scat prey item, and the cluster time for T_2 is < 12h, then the prey remains of the previous cluster T_1 was checked. If the scat prey item was the same species as the prey remains at T_1 and the time difference between the clusters was within the gut transit time limit (i.e., 0.5 or 4 days), then the scat prey item was a duplicate feeding event (of the T_1 cluster prey remains; **V**). If the time difference was outside of the gut transit limit, then the scat prey item was a missed feeding event (**VI**). If the prey remains at T_1 were different from the scat prey item, then it was a missed feeding event (**VII**). If there are prey remains present at T_2 and they are the same species as the scat prey item and the cluster time for T_2 is > 12h then it is a duplicate feeding event (of the T_2 cluster prey remains; **VIII**). If the scat prey item species was the same as both the T_1 cluster prey remains and the T_2 previous cluster prey remains then the age of the scat was used to decide which feeding event it belonged to: if the scat was old, then it was assigned to T_2 and if it was fresh then it was assigned to T_1.

PREY CLASSIFICATION, OCCURRENCE AND BIOMASS CALCULATION

All prey species were classified into three categories: i) *wild* prey species indigenous to the Peninsula, ii) *synanthropic* prey species that are indigenous but which are known to thrive in human-modified landscapes (*sensu* Johnston 2001) and iii) *exotic* introduced prey species, such as domestic dogs (*Canis lupus familiaris*) and cats (*Felis catus*), livestock such as goats (*Capra aegagrus hircus*), sheep (*Ovis aries)*, various poultry, and introduced rodents (e.g., brown rats and grey squirrels). I calculated corrected frequency of occurrence (CFO) per scat, and the mean biomass for each of the three prey categories, for both scats and clusters. I then calculated proportion edible mass of prey remains found using proportions scaled to equivalent prey mass categories (see Funston et al. 1998 Appendix 1). The proportions for use in caracals were adapted from Grobler's (1981) feeding observations. Specifically, prey species with a mass < 0.05 kg were 100% consumed, 0.05 – 0.25 kg were 90% consumed, 0.26 – 2.5 kg were 67% consumed and > 2.5 kg were 60% consumed. I determined prey masses by multiplying mean adult female mass (Skinner & Chimimba 2005, Hockey et al. 2005) by 0.75 to account for an assumed proportion of predation on juvenile individuals, as used for previous carnivore diet studies (e.g., African lion, *Panthera leo*, Hayward & Kerley 2005; leopard, Hayward et al. 2006). Where the exact species identification was unknown, the average mass for that prey group was used.

The prey items present in the scat are reported as measures of frequency of occurrence to allow for comparisons with previous studies (Klare et al. 2011). This included frequency of occurrence per food item ("relative occurrence", RO) and corrected frequency of occurrence per scat (CFO). To estimate consumed biomass, I used the generalised felid biomass model developed by Chakrabarti et al. (2016). The model requires only the mean predator mass (calculated as the mean mass of the caracals in the diet study), number of scats containing the prey item (calculated by summing the proportional amounts of each prey item found in the scat, i.e., CFO) and 0.75 mean female prey mass (from Skinner & Chimimba 2005, Hockey et al. 2005) as inputs.

STATISTICAL ANALYSES

To examine diet sampling efficiency I used the R package *vegan* (Oksanen et al. 2013). The bootstrap method of the "specpool" function was used to calculate extrapolated species richness in the species pool for each method (i.e., species identified through GPS cluster and scat analysis). To compare the similarity in the corrected frequency of occurrence (CFO) of prey items between scat and clusters, a Bray-Curtis similarity index was calculated, as it reflects quantitative similarity between communities (Bloom 1981). Equivalent frequencies of prey between methods represent a Bray-Curtis similarity coefficient of 1.

Chi-squared tests were used to determine if species composition differed between i) scat samples collected opportunistically versus those found at GPS clusters, ii) prey remains located at GPS clusters versus

all scat samples found, and iii) prey remains found at GPS clusters versus prey remains found at GPS clusters that are integrated with scat samples (integrated-diet) using both minimum and maximum gut transit times. To test for differences in biomass consumed between the two methods (scat and GPS cluster analysis) and the three prey categories (wild, synanthropic and exotic) I used unbalanced Type III two-way ANOVAs for: i) prey remains found at GPS clusters versus all scat samples found, ii) prey remains found at GPS clusters versus prey remains found at GPS clusters integrated with scat samples collected at GPS clusters (integrated-diet) for minimum and maximum gut transit times. To test for differences in biomass consumed between the three GPS cluster fix rates (3-hour, 20-minute, and a combination of both) I used an unbalanced Type III one-way ANOVA. The consumed biomass data was non-normal and lacked homogeneity of variance and was therefore log-transformed to fulfil ANOVA assumptions. Tukey HSD post hoc tests were performed for each ANOVA to find means for the categories that were significantly different.

To determine how sampling changed with distance from urbanisation, I compared the proportion of scat, GPS clusters with prey remains, and feeding events from the integrated-diet method (4-day) at 50 m bins of distance from the urban edge. The availability of wildland habitat on the Peninsula was measured by laying a grid of 10 m cells on the clipped area of non-urban habitat patches in ArcGIS (v. 10.1; ESRI 2010) and the number of 10 m cells which fell into the same bins of Euclidean distance from the urban edge was calculated.

Finally, to test for specific bias in each method used, I resampled (1,000 iterations) the prey group of interest (i.e., wild, synanthropic and exotic) by caracal to quantify if sampling was biased by specific individuals (Balme et al. 2019). To evaluate if site accessibility and safety biased my findings, I also resampled the data by binned (100 m) distances to urban edge. I further investigated potential spatial bias in the clusters investigated compared to those that were not investigated by testing for a difference in distance from the urban edge using a bootstrap hypothesis testing approach (10,000 iterations). All analyses were conducted in R v3.5.1 (R Core Team 2020) using preloaded packages.

RESULTS

SAMPLING

The mean duration that the 26 collared individuals were tracked was 154 ± 96.7 SD days. Of these, 22 caracals produced clusters that were feasible to visit given the safety constraints of my study area (Table 2.1; Fig. 2.2). A total of 4,202 clusters were generated between November 2014 and November 2016 with a mean fix success of 99.2%. A total of 677 GPS clusters were investigated (mean fix success = 98.9%), which represented 16.11% of the overall clusters generated. I found a high proportion of all generated clusters were ≥ 12 hours in duration (29.53%), while almost half (45.4%) of investigated clusters were ≥ 12 hours. Most

generated clusters (56.47%) were formed during 3-hour sampling intervals. Twenty-minute locations (for a consecutive 24 – 36 hours) were collected only every 9th – 10th day, and I rarely documented multiple clusters within a 24 – 36-hour period. Nevertheless, 27.15% of clusters were formed during the 20-minute sampling interval and 15.17% were a combination of both schedules. The mean time difference between the date of cluster formation and the date of investigation was 16 days ± 10 SD (range: 1 – 83 days). Of the 677 GPS clusters investigated, 36.3% of GPS clusters were for females and 63.07% were for males; 89.21% were for adults and 10.79% were for subadults (Table 2.1). Feeding sites were located at 241 clusters (35.75% of all clusters; Table 2.1).

Table 2.1 A summary of the diet dataset including data obtained from collared caracals for which GPS clusters were investigated (n = 22), and opportunistically collected scat samples and prey remains on the Cape Peninsula, South Africa.

Sample type	Total count of prey items	Adult female (n=8)	Subadult female (n=1)	Adult male (n=8)	Subadult male (n=5)
SCAT	**654**				
Scat at clusters	**328**	**97**	**22**	**186**	**23**
With prey remains	177	55	6	144	2
Without prey remains	151	42	16	72	21
Opportunistic scat	**326**	**NA**	**NA**	**NA**	**NA**
Field	311	NA	NA	NA	NA
Capture	12	3	2	5	2
Necropsy	3	1	0	0	2
CLUSTERS	**677**	**226**	**30**	**360**	**61**
With prey remains	241	81	10	134	16
Without prey remains	436	145	20	226	45
PREY REMAINS	**385**				
Prey remains at clusters	**331**	111	15	190	15
Opportunistic prey remains	**54**	NA	NA	NA	NA

Resting beds and scratching posts were also identified at clusters (Table 2.2) with 37.08% of GPS clusters showing no evidence of feeding, resting or territorial behaviour (Table 2.2). Of the 242 GPS clusters with prey remains, 66.4% were formed on the 3-hour GPS fix interval, 13.7% on the 20-minute fix interval and 19.9% were a combination of both fix intervals. Of all clusters investigated 51.55% were within 500 m of the urban edge and of these, 60.99% had prey remains. I found that 58.61% of clusters with prey remains were within 500 m of the urban edge, while the cumulative percentage of available wildland habitat within 500 m was 26.60% (Fig. 2.4, black dotted line). Further, 40.79% of clusters with prey remains were within 200 m of the urban edge (Fig. 2.4, purple line), although the cumulative percentage of available wildland habitat within 200 m was only 12.55% (Fig. 2.4, black dotted line).

Table 2.2 Foraging and resting site data collected for collared caracals (n = 22) of different age and sex classes for which GPS clusters (n = 677) were investigated on the Cape Peninsula, South Africa; mean ± SD (*n*).

Group	Days tracked	Clusters investigated	Scats collected	Prey remains collected	Resting beds	Scratching posts	Empty GPS clusters
Adult female (n = 8)	149.3 ± 114.8 (1350)	28.3 ± 32.3 (226)	12.1 ± 12.4 (97)	16 ± 16.9 (82)	5.6 ± 5.9 (37)	0.4 ± 0.7 (3)	11.9 ± 15.8 (95)
Subadult female (n = 1)	185.0 (185)	30.0 (30)	22.0 (22)	16.0 (16)	2.0 (2)	2.0 (2)	5 (5)
Adult male (n = 8)	210.6 ± 102.8 (1900)	45.0 ± 31.5 (360)	23.3 ± 22.5 (186)	25.0 ± 20.4 (133)	7.8 ± 4.9 (58)	1.0 ± 1.1 (8)	16.9 ± 11.5 (135)
Subadult male (n = 5)	97.2 ± 32.3 (586)	12.2 ± 12.1 (61)	4.6 ± 5.7 (23)	4.6 ± 5.7 (16)	2.0 ± 2.0 (10)	0.0 ± 0.0 (0)	3.8 ± 3.3 (19)

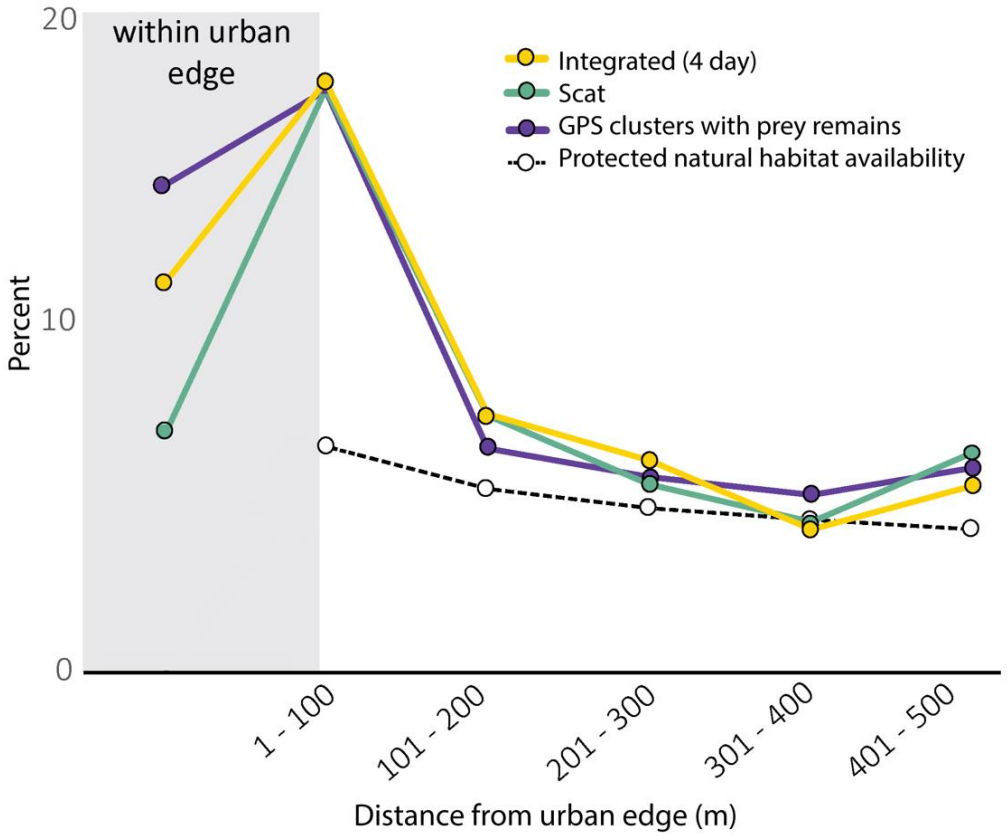


Fig. 2.4 Percentage of prey items found at binned distance categories from the urban edge (m) for each method (GPS clusters with prey remains, scat, and the integrated-diet method with the maximum 4-day gut transit time). The dotted black line shows the percentage of wildland habitat availability (see *Methods*).

A total of 654 caracal scat samples were collected, of which 177 scat samples were found at GPS clusters with prey remains, 151 scat samples from GPS clusters without prey remains and 326 scat samples from locations not associated with GPS clusters (i.e., opportunistically, Table 2.1). The proportion of exotic and synanthropic prey was marginally higher in scat samples collected at GPS cluster sites than those collected independently of GPS cluster investigations (i.e., opportunistically, χ^2_2=5.72, P = 0.06).

Given that only a fraction of generated clusters was visited (16.11%), I evaluated the dataset for potential biases that may have arisen from a lack of representative sampling. My resampling suggests that

there is little evidence of individual bias in the three methods (GPS cluster prey remains, scat, and integrated-diet method). Prey group proportions remained similar to those found across resampling events, with low variance, suggesting that individual caracals did not bias these prey group categories (Table 2.3).

Table 2.3 Caracal diet estimates from collared individuals (n = 22) on the Cape Peninsula, South Africa for three prey groups (wild, synanthropic, exotic) using four methods (prey remains found at GPS clusters, scat found at GPS clusters, an integration of these two estimates at maximum, 4-day, and minimum, 0.5-day, gut transit limits; see *Methods*) with bootstrapped estimates (mean ± SD; 1,000 iterations).

Prey group	GPS cluster prey remains method (n = 331)	Bootstrap estimates	GPS cluster scat analysis method (n = 443)	Bootstrap estimates	Integrated-diet method (4-day, n = 731)	Bootstrap estimates	Integrated-diet method (0.5-day, n = 739)	Bootstrap estimates
Wild	0.408	0.467 ± 0.017	0.822	0.77 ± 0.017	0.651	0.624 ± 0.018	0.651	0.626 ± 0.017
Synanthropic	0.465	0.390 ± 0.018	0.094	0.067 ± 0.013	0.250	0.233 ± 0.017	0.252	0.234 ± 0.016
Exotic	0.127	0.141 ± 0.012	0.083	0.156 ± 0.013	0.098	0.142 ± 0.013	0.097	0.140 ± 0.013

Similarly, resampling by binned distance from urban edge resulted in similar prey group proportions (Table 2.4), which suggests that distance from the urban edge did not bias these prey categories. Additionally, there was little evidence to suggest a significant difference in distance from the urban edge between all generated (mean = 2,602.8 m) and investigated clusters (mean = 2,930.9 m; bootstrapped [10,000 iterations] t = -0.243, $P = 0.56$).

Table 2.4 Caracal diet estimates on the Cape Peninsula, South Africa for three prey groups (wild, synanthropic, exotic) using four methods (prey remains found at GPS clusters, scat found at GPS clusters, an integration of these two estimates at maximum, 4-day, and minimum, 0.5-day, gut transit limits, see *Methods*) with bootstrapped estimates (mean ± SD, 1000 iterations) categorised by 100 m bins of distance to the urban edge (m).

Prey group	GPS cluster prey remains method (n = 331)	Bootstrap estimates	GPS cluster scat analysis method (n = 443)	Bootstrap estimates	Integrated-diet method (4-day, n = 731)	Bootstrap estimates	Integrated-diet method (0.5-day, n = 739)	Bootstrap estimates
Wild	0.408	0.336 ± 0.037	0.822	0.793 ± 0.034	0.651	0.410 ± 0.035	0.651	0.410 ± 0.038
Synanthropic	0.465	0.540 ± 0.041	0.094	0.109 ± 0.027	0.250	0.483 ± 0.037	0.252	0.482 ± 0.039
Exotic	0.127	0.123 ± 0.028	0.083	0.098 ± 0.025	0.098	0.107 ± 0.025	0.097	0.107 ± 0.026

Occurrence, biomass and species richness estimates using scat and GPS cluster methods

There were significant differences in both dietary composition (χ^2_2=737.58, *P* <0.001, Fig. 2.5) and biomass (F_1 = 76.9, *P* < 0.001, Fig. 2.6) estimates of prey types for GPS clusters and scats with a relatively low overall similarity between the methods (Bray-Curtis = 0.64). In terms of biomass, no significant difference was found between exotic, synanthropic, and wild prey types (F_2 = 1.2, *P* = 0.30, Fig. 2.6). However, the interaction between the method and prey type was highly significant (F_2 = 10.22, *P* <0.001). A Tukey HSD post-hoc test indicated that for scat analysis, biomass estimates were significantly higher in wild versus synanthropic prey (*P* < 0.001), while there were no significant differences between any other prey categories, nor between any prey categories for the GPS cluster analysis (Fig. 2.6).

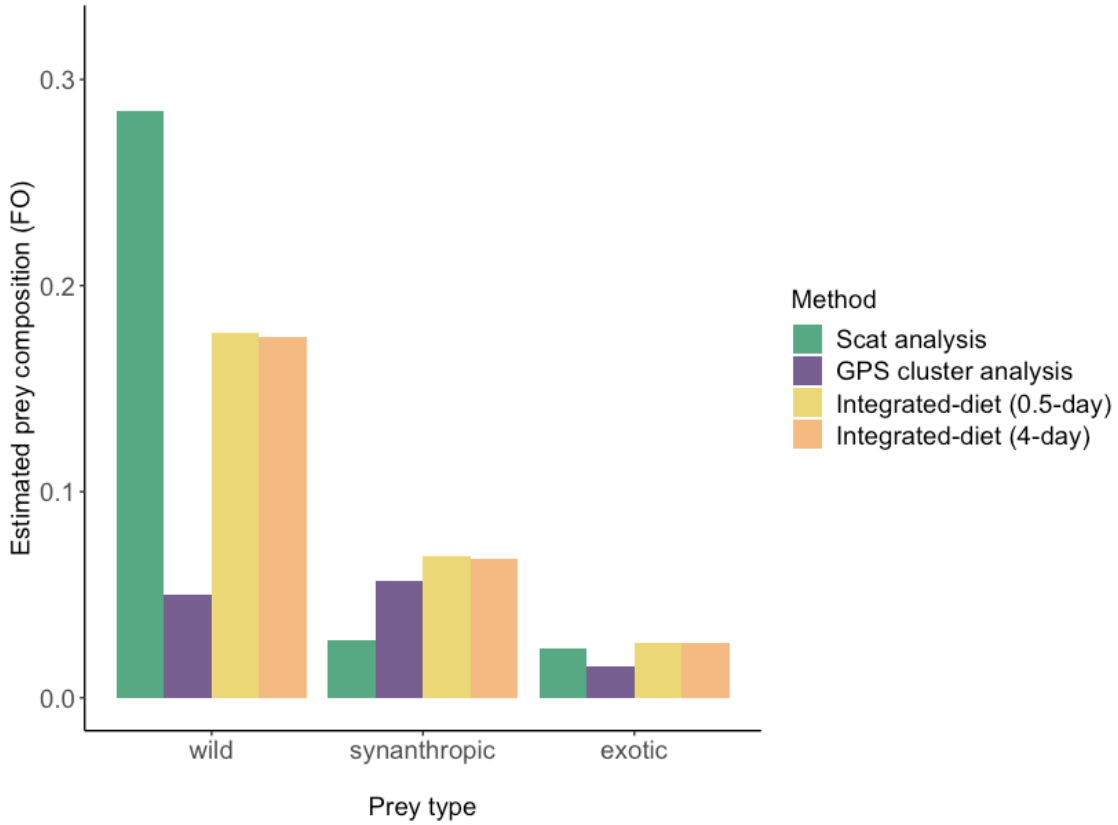


Fig. 2.5 Bar plot of estimated caracal dietary composition (FO, frequency of occurrence) using scat analysis, GPS cluster analysis and GPS-located prey remains integrated with minimum transit (0.5-day) and maximum transit time (4-day) scat samples for prey belonging to three prey categories (*wild, synanthropic* and *exotic*) from caracal (n = 22) on the Cape Peninsula, Western Cape, South Africa.

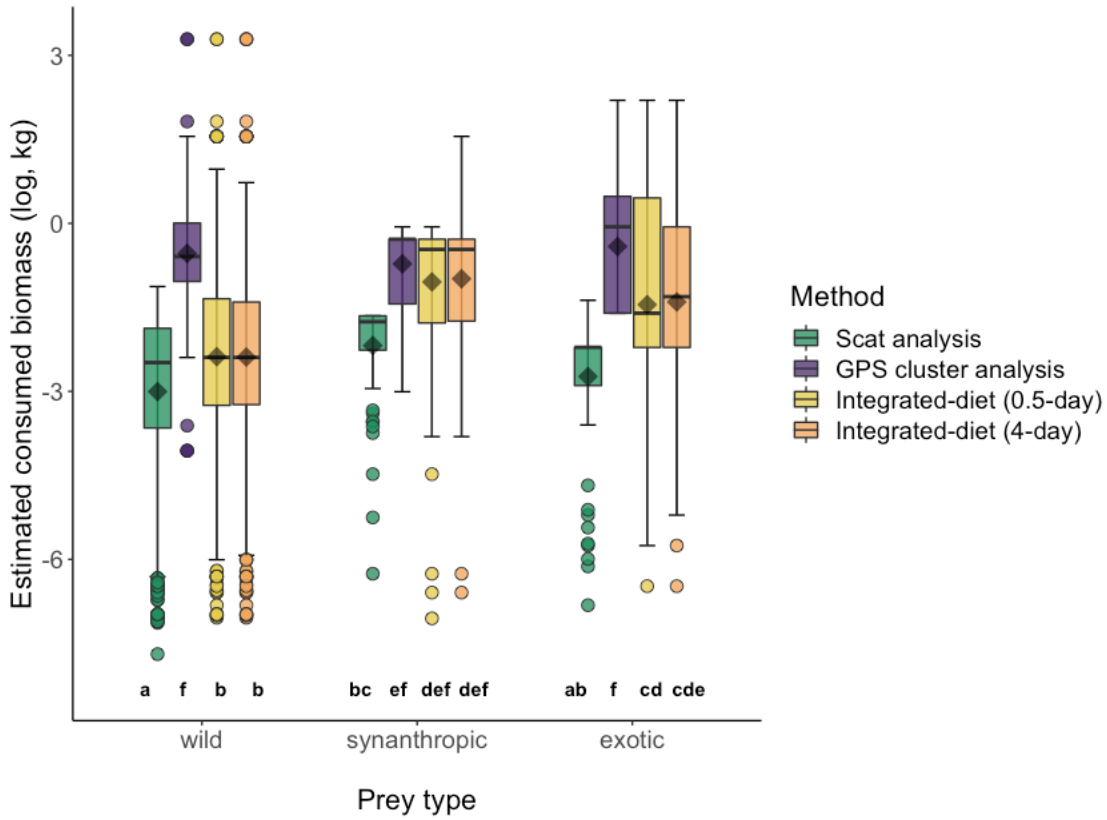


Fig. 2.6 Boxplots (median, interquartile range, and upper and lower quartile; diamonds = means) of estimated caracal prey consumed biomass (kg, log-transformed) using scat analysis, GPS cluster analysis, GPS-located prey remains integrated with minimum transit (0.5-day) and maximum transit time (4-day) scat samples for prey belonging to three prey categories (*wild, synanthropic* and *exotic*) from caracal (n = 22) on the Cape Peninsula, Western Cape, South Africa. Letters indicate significant differences determined by post-hoc Tukey HSD tests.

Strikingly different dietary estimates were derived from scat compared to GPS clusters. Small mammals (mainly rodents 0.005 – 0.11 kg) were the dominant species detected in scat. Birds (0.02 – 1.12 kg) were the dominant prey detected at clusters. Unexpectedly, the smallest prey species detected at 3-hour interval clusters were mammals (< 0.02 kg) and birds (< 0.03 kg). Although small prey items were detected at clusters, given the coarse sampling intervals, it is likely more feeding events with prey of similar size were missed. Using the GPS cluster method (n = 296), I detected 58 unique prey species (see full list in Appendix 2.1) with an additional 10 species that were likely undetected following the species accumulation bootstrap. Dominant avian species included: Helmeted guinea fowl (17%), Cape cormorant (*Phalacrocorax capensis,* 11%) and Egyptian goose (10%; Fig. 2.7). Frequency of occurrence (RO) estimates per prey item revealed that synanthropic birds were the most consumed (44.94%), while biomass estimates show wild mammals to be most common (44.85%, Table 2.5). Exotic prey comprised < 20% using both prey remains RO (12.73%) and biomass (15.79%) estimates (Table 2.5).

In contrast, when examining scat, I detected 59 species (see full list in Appendix 2.1) with bootstrap estimates indicating only five species were likely undetected. Rank abundance indicated that vlei rat (*Otomys irroratus,* 22%), Cape cormorant (10%), and rock hyrax (*Procavia capensis*, 8%) were the most dominant

species in scat (Fig. 2.7). According to all scat estimation methods (RO, CFO, and biomass) most prey were wild mammal species (> 49%; Table 2.5) with exotic prey < 10% (Table 2.5). Prey biomass in scat revealed higher use of wild prey (20.8% more), while caracal prey remains found in the field revealed greater use of urban (8.4% more) and synanthropic avian prey (12.4% more; Table 2.5). Specifically, I find that from all prey remains found in the field, 6.23% of caracal diet was made up of domestic animals, while in scat only 1.53% of caracal diet was represented by domestic animals.

Table 2.5 Caracal prey on the Cape Peninsula, South Africa as determined by scat analysis and kill sites identified using GPS cluster analysis for three prey categories (*wild, synanthropic* and *exotic*). "All scat" includes scat found at GPS clusters and opportunistically; "all prey remains" includes prey remains found at GPS clusters and opportunistically. The results of the integrated method (both scat and prey remains found at GPS clusters integrated, see *Methods*) are presented at both minimum 0.5-day gut transit and maximum 4-day gut transit limits.

	ALL SCAT (n=913)				ALL PREY REMAINS (n=385)			INTEGRATED (0.5-day, n=739)			INTEGRATED (4-day, n=731)		
Prey group	**Count of prey items**	**RO**	**Correct-ed FO**	**% Biomass**	**Count of prey items**	**RO**	**% Biomass**	**Count of prey items**	**RO**	**% Biomass**	**Count of prey items**	**RO**	**% Biomass**
Wild	**772**	**84.56**	**82.37**	**81.02**	**163**	**42.34**	**60.25**	**481**	**65.09**	**59.03**	**476**	**65.12**	**58.78**
amphibian	2	0.22	0.33	0.21	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
bird	207	22.67	25.61	27.32	112	29.09	15.32	174	23.55	15.92	172	23.53	22.16
insect	13	1.42	0.98	0.52	0	0.00	0.00	7	0.95	0.08	7	0.96	0.08
mammal	513	56.19	53.01	49.76	50	12.99	44.85	279	37.75	42.57	276	37.76	36.09
reptile	37	4.05	2.45	3.21	1	0.26	0.08	21	2.84	0.45	21	2.87	0.46
Synanthropic	**76**	**8.32**	**9.79**	**11.57**	**173**	**44.94**	**23.97**	**186**	**25.17**	**27.27**	**183**	**25.03**	**28.13**
bird	76	8.32	9.79	11.57	173	44.94	23.97	186	25.17	0.00	183	25.03	0.00
Exotic	**65**	**7.12**	**7.84**	**7.42**	**49**	**12.73**	**15.79**	**72**	**9.74**	**13.70**	**72**	**9.85**	**13.09**
bird	3	0.33	0.39	0.29	23	5.97	2.57	21	2.84	2.99	21	2.87	2.94
mammal	62	6.79	7.45	7.13	26	6.75	13.21	51	6.90	10.71	51	6.98	10.15

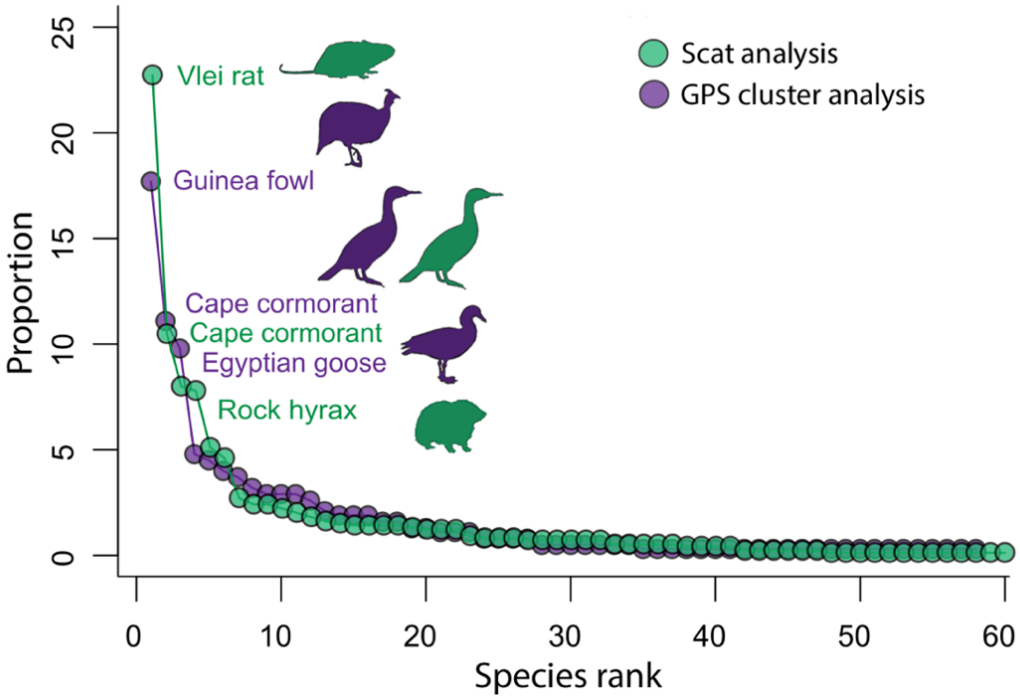


Fig. 2.7 Rank abundance plots for prey items identified to species level per GPS cluster with prey remains (n=296) and per scat (n = 590). Helmeted guinea fowl (*Numida meleagris*), Cape cormorant (*Phalacrocorax capensis*) and Egyptian goose (*Alopochen aegyptiaca*) were the most dominant species for prey remains. Vlei rat (*Otomys irroratus*), Cape cormorant and Rock hyrax (*Procavia capensis*) were the dominant species present in scat.

A post-hoc Tukey HSD test showed a significant difference ($P < 0.05$) in prey biomass between GPS clusters identified using the combined fix intervals and the fine scale (20-minute) fix interval. There was no significant difference in the prey biomass between the coarse (3-hour) and fine scale (20-minute) fix clusters, or the coarse and combined fix interval clusters (Fig. 2.8).

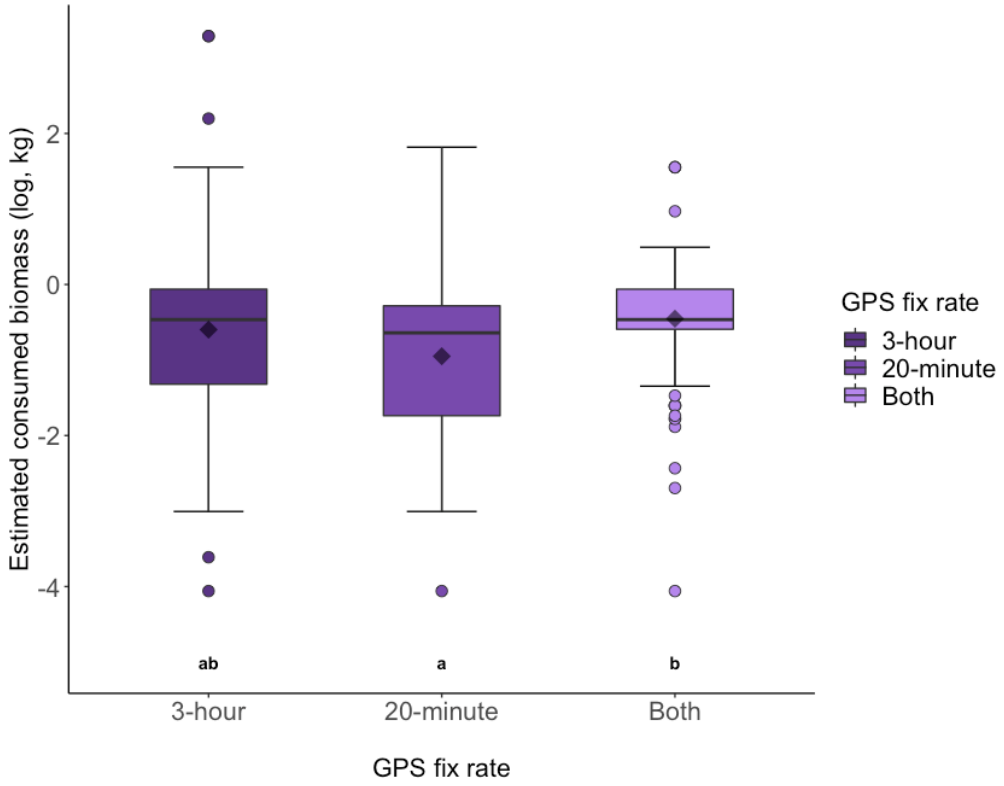


Fig. 2.8 Boxplots (median, interquartile range, and upper and lower quartile; diamonds = means) of estimated caracal prey biomass (kg, log-transformed) using GPS cluster analysis for three fix rates (3-hour, 20-minute and clusters formed using both fix rates) of collared caracal (n = 22) on the Cape Peninsula, Western Cape, South Africa. Letters indicate significant differences determined by post-hoc Tukey HSD tests.

INTEGRATING SCAT AND GPS CLUSTER ANALYSIS DATA WITH GUT TRANSIT TIMES

Prey items found in scat samples collected at GPS clusters (n = 443), and the prey remains detected at GPS clusters rarely matched (only 6.09% [n = 27] of samples). Prey items found in scat matched prey remains found at previous GPS cluster feeding sites only 1.8% (minimum transit 0.5-day, n = 8) and 3.61% (maximum transit 4-day, n = 16) of the time, indicating that scats found at GPS clusters reflect missed feeding events rather than duplication of feeding events. In total, I recorded between 7.90% (minimum transit, 0.5-day, n = 35) and 9.71% (maximum transit, 4-day, n = 43) duplicate feeding events. Using the integrated-diet method, I estimate the number of missed feeding events to be 400 and 408 for maximum and minimum gut transit times, respectively. Therefore, after using this integration approach, feeding events increased by 54.71% (maximum transit, 4-day, n = 731) or 55.21% (minimum transit, 0.5-day, n = 739). According to both RO and biomass estimates at both gut transit time limits, most prey were wild mammal and synanthropic bird species, and exotic prey were < 14% of all biomass consumed (Table 2.5).

The inclusion of missed feeding events altered the estimation of urban prey consumed. There was a significant difference between estimated dietary compositions when comparing GPS cluster analysis with the integrated-diet method at both maximum (4-day: $\chi^2_2 = 184.26$, $P < 0.001$, Fig. 2.5) and minimum gut transit times (0.5-day: $\chi^2_2 = 185.46$, $P < 0.001$, Fig. 2.5). I found that for both minimum (0.5-day) and maximum (4-

day) gut transit limits there were significant differences in biomass between the GPS cluster method and the integrated-diet method ($F_2 = 6.98$, $P < 0.01$, Fig. 2.6), with mean biomass estimates being lower for the integrated-diet method. The majority of missed feeding events were prey items weighing < 0.5 kg (57.70% at minimum [0.5-day] and 58.60% at maximum [4-day] gut transit limit). Overall, there was no significant difference in biomass between exotic, synanthropic and wild prey ($F_2 = 2.97$, $P = 0.40$, Fig. 2.6). However, the interaction between method used (i.e., GPS cluster analysis or the integrated-diet method at either gut transit limit) and prey category was highly significant ($F_4 = 14.24$, $P < 0.001$). Importantly, Tukey HSD post-hoc tests showed significantly higher exotic than wild prey biomass ($P < 0.001$) and higher synanthropic than wild prey biomass ($P < 0.001$) when integrating methods at both minimum and maximum gut transit limits (Fig. 2.6). In contrast, there were no significant differences in biomass between prey categories for the GPS cluster method (Fig. 2.6) at either gut transit limits, indicating that these differences only arose using the integrated-diet approach.

DISCUSSION

Caracals are generalist and opportunistic predators that thrive in human modified landscapes of the Western Cape province of South Africa (Stuart 1982; Avenant and Nel 2002). Similar to caracal diet studies in both protected and small livestock farming areas (Palmer and Fairall 1988; Stuart and Hickman 1991; Avenant and Nel 2002; Melville et al. 2004; Braczkowski et al. 2012; Drouilly et al. 2017), I found that caracals have a diverse diet but that estimates varied considerably with the method and analyses used. Given that smaller prey were likely to be missed by GPS cluster investigations and overestimated using scat analysis I adopted an integrated-diet approach to understand how caracals forage within and adjacent to a large city.

COMPARISON OF METHODS

Both the scat and GPS cluster approaches had inherent biases. The scat approach overestimated small mammal prey, while the GPS cluster approach overestimated larger, particularly avian, prey. The GPS cluster approach was likely further biased by the use of 3-hour fix intervals, which were too coarse to detect small prey. An intuitive solution to the detection bias inherent in GPS cluster analysis would be to increase the fix interval of GPS-collars and investigate more clusters formed during shorter time intervals. I acknowledge that the 3-hour sampling interval provided only a crude estimate of the cluster centroid, and to compensate for uncertainty in the "activity centroid" of each cluster, search efforts were dispersed over an area of 7,854 m^2 (i.e., 50 m radius from centroid estimate). Higher intensity sampling frequency is becoming more feasible with advancing technology, and movement data can now be collected in by-the-minute resolution, even for medium-sized carnivores (Svoboda et al. 2013; LaPoint et al. 2015; McCann et al. 2018; Studd et al. 2021; Serieys et al. 2021). With higher resolution (5- to 10-minute) sampling intervals, there may have been more success in locating the true centroid of activity, and thus concentrating search efforts to a smaller area and discovering the remains of smaller prey. Further, with extremely fine-scale data, each cluster investigation takes less time because search efforts are reduced (L. Serieys, *pers. Comm.*), thus facilitating the investigation of substantially more clusters.

Despite these potential advantages to finer-scale GPS data to locate feeding sites, I did not find a significant difference in estimates of biomass consumed when comparing coarse- and fine-scale GPS fix intervals for Peninsula caracals. These findings suggest that finer-resolution sampling on the order of 20-minute fix intervals did not aid in the detection of smaller prey items for caracals in my study area, although there was less opportunity to investigate 20- minute clusters given that 20- minute data were collected infrequently (every 9 – 10^{th} day) compared with daily sampling of 3-hour locations. However, going forward, for those studies heavily focused on the diet of smaller carnivores, I would recommend finer-scale sampling on the order of minutes rather than hours. An additional constraint that may have affected cluster sampling is

the avoidance of two small unsafe areas, although I found little evidence to suggest the subsample of clusters that were investigated were non-representative.

PREY RESOURCES AT THE URBAN EDGE

While urban development is associated with high extirpation rates of indigenous fauna (McKinney 2002), select native synanthropic species may thrive in human modified landscapes. The increased abundance of a few synanthropic species may be sufficient to support numerous predatory species – coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), stone martens (*Martes foina*), Eurasian badgers (*Meles meles*), bobcats, and pumas all benefit from the increased abundance of indigenous and synanthropic prey at the urban edge (Bateman and Fleming 2012), while rarely predating domestic animals (MacCracken 1982; Quinn 1997; Fedriani et al. 2001; Contesse et al. 2004; Morey et al. 2007; Riley et al. 2010). Data on prey distribution and abundance across the Peninsula study area are limited and were beyond the scope of this study. It is thus not known whether caracals are selecting for certain prey or simply consuming them in accordance with their relative abundance. However, opportunistic generalist predators, such as caracals, forage most frequently on those prey species are most abundant on the landscape (Avenant and Nel 2002) and predatory species forage in areas that offer better resources for their prey (Newsome et al. 2015b; Smith et al. 2019a). Most of the natural land on the Peninsula falls within the Table Mountain National Park and is at a higher altitude than urban and rural areas. The urban edge is thus invariably the lowest natural land available to most wildlife species and for that reason is predicted to be more productive than land further from the urban edge. Overall, my findings support this, with almost 60% of all foraging clusters occurring within 500 m of the urban edge where prey species are likely more abundant. Indeed, commonly consumed avian prey have been recorded as more abundant at the urban edge of Cape Town (e.g., rock pigeons, *Columba livia*, and Guinea fowl, Suri et al. 2017).

Caracals are occasionally identified as having a negative impact on communities within Cape Town, with the predation of domestic cats being particularly commonplace (Nattrass and O'Riain 2020). Despite this and the high frequency of foraging close to urban areas, my integrated-diet approach revealed that very little of caracal diet was represented by exotic animals (< 14%, with < 4% domestic animals) that in turn likely capitalise on increased resources at the urban edge.

THE VALUE OF AN INTEGRATED-DIET APPROACH

My integrated-diet approach confirmed that caracals living adjacent to urban areas are generalist, opportunistic predators similar to those living in natural and rural landscapes (e.g., Avenant and Nel 2002; Braczkowski et al. 2012). Perhaps more importantly, my study design has led to new insights on how best to

quantify the diet of a medium-sized carnivore. First, even with coarse (3-hour) fix intervals, GPS clusters were clearly identifiable on the landscape, and I detected avian prey remains at clusters that were underrepresented in scat. Caracals, like many other medium-sized felids (Elbroch 2003), pluck feathers prior to consuming avian prey (Grobler 1981) and large, easily visible feathers remained at clusters long after consumption. The act of plucking feathers means they ingest few that would be detected in scat or stomach contents (e.g., Stuart and Hickman 1991). Second, when implementing the integrated-diet approach, the total count of feeding events more than doubled. Further, duplicate feeding events were rare, suggesting the integrated-diet approach seldom results in pseudo-replication. Rather, a substantial number of missed feeding events are revealed. Finally, there were significant shifts in biomass estimates of each prey category (exotic, synanthropic, and wild) when the integrated-diet approach was used, and the differences in biomass became significant only with the addition of scat prey items, specifically due to improved detection of smaller prey.

A potential issue with the integrated-diet method is the marginally significant difference between scats found at GPS clusters and those found opportunistically (i.e., without caracal individual information), suggesting there may be an issue with excluding these opportunistic scats, as this may alter prey group proportions. This difference may be the result of insufficient sampling of opportunistic scat, particularly closer to the urban edge. A solution may be to use DNA sequencing methods to determine their source individual, but this may be cost prohibitive (Taberlet et al. 1999; Farrell et al. 2000; Adams and Waits 2007). Overall, as reported by other studies comparing scat and cluster findings (Marucco et al. 2008; Martins et al. 2011; Tambling et al. 2012; Pitman et al. 2014; Perilli et al. 2016; Drouilly et al. 2019), I find that each approach offers unique information. Therefore, systematically integrating both GPS-collar cluster data with scat data, and correcting for gut transit times, yields a more comprehensive diet assessment than either approach in isolation, despite the increased costs (to the animal and financially) of deploying GPS-collars.

Risks of consuming urban edge prey

While Peninsula caracals rarely consumed exotic species, a recent study showed that 92% of caracals (n = 24) were exposed to the ubiquitous second-generation rodenticides in and around Cape Town (Serieys et al. 2019). Thus, my results on limited consumption of exotic prey, specifically very few targeted exotic rodents, point to widespread exposure of native prey species to these rat poisons, or to caracal tertiary exposure via other more urban-associated carnivores that frequently consume exotic rodents (e.g., large-spotted genets, *Genetta tigrina*; Widdows and Downs 2015, 2018) and are also exposed to poisons (Serieys et al. 2019). Disease spillover may also occur between domestic and free-ranging carnivores (Riley et al. 2004; Bevins et al. 2012; Carver et al. 2015) and within the Peninsula, our research group has observed alarming mortality rates that I suspect are linked with both pesticide (e.g., Serieys et al. 2019; Chapter 4) and pathogen

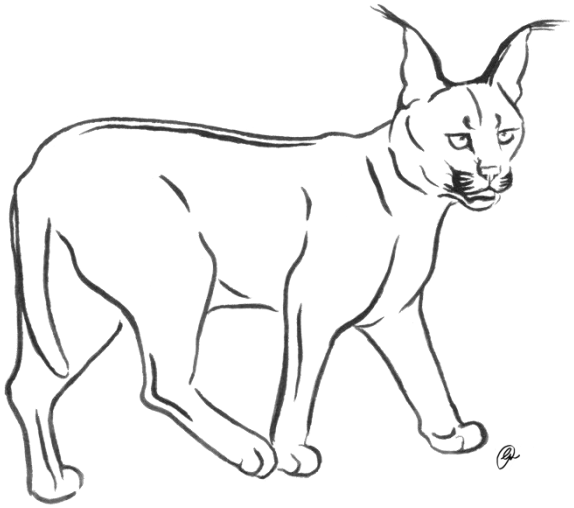
exposure (Viljoen et al. 2020; L. Serieys et al., *unpub. data*). Although I show that caracals rarely prey on domestic cats or dogs, what limited spillover does occur during predation events may substantially threaten Peninsula caracals.

CONCLUSIONS

Overall, these findings highlight the importance of an integrated-diet approach to foraging studies, particularly for medium-sized carnivores. I found that not only do the independent scat and GPS cluster methods produce consistently different estimates of caracal diet, but a valuable proportion of feeding events go undetected. The results of diet studies have important downstream implications for research that may form the foundation of management practices. Specifically, dietary data are often used to calculate resource selection functions (RSFs; Manly et al. 2002; Benson et al. 2016; Smith et al. 2016) that are influenced by the model input, specifically the location of feeding events and the prey species. Diet estimations, such as those I obtained from either scat analysis or GPS cluster analysis alone, could therefore inherently skew resource selection estimates. This may be especially problematic for mesocarnivore species that are often used as landscape species (Sanderson et al. 2002; Redford et al. 2003), particularly in urbanising, fragmented landscapes. The integrated-diet approach I present, while not entirely eliminating bias, could nevertheless provide a more complete understanding of diet of medium-sized carnivores, and subsequently, resource selection. Further, caracals are a potentially valuable indicator of trophic dynamics and threats in this global biodiversity hotspot (Myers et al. 2000; Sergio et al. 2006). Their conservation in this urbanising landscape is a priority, and the improved understanding of their diet provided here will facilitate informed management decisions.

CHAPTER 3

HIDING IN PLAIN SIGHT: SPATIOTEMPORAL RISK MITIGATION BY CRYPTIC CARACALS FORAGING AT CAPE TOWN'S URBAN EDGE



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ABSTRACT

As natural habitats are progressively transformed, effective wildlife conservation will increasingly rely on understanding the phenotypic traits that allow select species to persist outside of protected areas. Through behavioural flexibility such species may trade off the benefits of abundant resources in human-modified landscapes with higher risks, both real and perceived. As highly adaptable species, caracals provide an opportunity to examine how medium-sized carnivores may adjust their foraging strategies relative to high-risk developed areas. Here I investigated caracal resource selection across a gradient of urbanisation in and around the city of Cape Town, South Africa. I use GPS cluster-located feeding events (n = 326 prey remains, n = 384 scat) and resting sites (n = 177), as response variables using a GLMM approach to understand factors affecting resource selection. I also examined spatial and temporal risk mitigation strategies by assessing behaviours at feeding clusters. Within their home ranges, caracals living in the urban-dominated region of the Cape Peninsula (n = 14; 548 feeding events) select for the urban edge, while caracals in the wildland-dominated region (n = 3; 162 feeding events) appear to avoid it. Adults selected for foraging at the urban edge more in comparison to subadults and may competitively exclude them from associated resources. By including back-traced scat feeding event locations, I was also able to improve the model resolution. I argue that, rather than flee, caracals foraging on the edge of a large metropole like Cape Town mitigate the risks associated with detection through a combination of remaining cryptic, prolonging handling time and maintaining high feeding site fidelity where cover is available. Along with their strong functional response to the urban edge, this strategy suggests that generalist carnivores like caracals may be drawn into, and stay longer, in areas with potentially increased prey availability despite the higher risks. While behavioural plasticity may facilitate carnivore coexistence with humans in urban ecosystems, it can also be maladaptive if it reduces fitness and leads the population into an ecological trap. I discuss mitigative recommendations to promote the conservation of caracal in this spatially isolated and rapidly urbanising landscape.

INTRODUCTION

In today's rapidly expanding cities, wildlife winners and losers are determined by their behavioural responses to the interplay of risk and reward within and adjacent to urban areas. Cities are highly challenging environments; they are noisy (Shannon et al. 2016), polluted (Serieys et al. 2015), fragmented by roads and other barriers (Crooks 2002), and support novel diseases (Bradley and Altizer 2007). Despite these challenges many urban areas sustain permanent wildlife communities (Shochat et al. 2006). As urban ecosystems expand, behaviourally flexible species must balance the possible advantage of increased foraging opportunities while developing behavioural strategies to mitigate anthropogenic risks (Lowry et al. 2013; Nattrass and Lusseau 2016; Fleming and Bateman 2018).

Urban-adapted species respond behaviourally to both direct risks, such as persecution due to human-wildlife conflict (Inskip and Zimmermann 2009), poaching (Kaltenborn and Brainerd 2016), and vehicle collisions (Seiler and Helldin 2006), and to perceived risks. For species that persist in human-dominated landscapes, fear of the "human apex predator" may elicit responses (Darimont et al. 2015; Smith et al. 2017) that can exceed that of even natural top predators (Clinchy et al. 2016). In doing so, fear responses, even to non-lethal activities, can cause a shift in behaviours to reduce exposure to human activities, with individuals seeking temporal or spatial refugia (Gaynor et al. 2018; Smith et al. 2019b; Nickel et al. 2020). For example, brown bears (*Ursus arctos*) avoid disturbed areas, especially during the day when human activity is high (Ordiz et al. 2014), while African lions (*Panthera leo*) hunt closer to human structures only at night (Suraci et al. 2019b), and bobcats (*Lynx rufus*), coyotes (*Canis latrans*; Murray and St. Clair 2015; Wang et al. 2015) and leopards (*Panthera pardus*; Odden et al. 2014) increase their nocturnality to avoid human activity. Even the recorded sound of human voices can lead to shifts in behaviour across trophic levels, causing carnivores to behave more cautiously and elusively (Suraci et al. 2019a). Numerous species also reduce movement rates (Tucker et al. 2018; Nickel et al. 2021) or increase vigilance (Benítez-López 2018) in human-dominated landscapes.

Avoidance strategies that mitigate direct and perceived risks can, however, be costly, particularly if animals adjust their behaviour while foraging (McNamara and Houston 1990; Houston et al. 1993). To avoid spatial overlap with human activity large carnivores may abandon kills altogether, thereby decreasing prey consumption time and reducing individual net caloric gain (Kerley et al. 2002; Smith et al. 2017). Temporal avoidance may also require increased bursts of rapid movement and less resting (Oriol-Cotterill et al. 2015a; Fehlmann et al. 2017). Together these behavioural changes may have adverse implications for foraging activity, reproduction and animal condition in wildlife species living in proximity to humans (Ditchkoff et al. 2006; Strasser and Heath 2013).

As urbanisation intensifies globally (Seto et al. 2012), understanding the behavioural strategies of species that persist in these landscapes is important for conserving urban biodiversity (Sol et al. 2013; Ritzel and Gallo 2020). Relative adaptability to human disturbance varies widely across species and populations. At the species level, habitat and dietary generalists demonstrate greater success in persisting in human-modified landscapes (Bateman and Fleming 2012; Fehlmann et al. 2020). Across populations, differences may depend on the level of exposure to disturbance (Benson et al. 2016; Ritzel and Gallo 2020), while within populations individual personalities and demographic factors may play important roles (Wolf and Weissing 2012; Miranda et al. 2013; Wat et al. 2020), with bolder individuals taking greater advantage of urban resources (Canestrelli et al. 2016; Breck et al. 2019). For example, female pumas (*Puma concolor*), lynx (*Lynx lynx*), and bobcats are more sensitive to urbanisation than males, while subordinate juveniles without defined home ranges are often pushed into marginal habitats by adults (Riley et al. 2003; Bouyer et al. 2015b; Smith et al. 2015). Where populations inhabit areas with high heterogeneity in landscape disturbance, individuals may adjust their

resource selection as a function of changes in local resource availability (Mysterud and Ims 1998). For example, pumas decrease their avoidance of some anthropogenic features as those features became more prevalent, thus increasing their potential to establish on the landscape (Knopff et al. 2014). This "functional response" (whereby animals adjust resource selection as a function of changes in local resource availability) can reveal both associated benefits and risks of a given habitat, and provide insight into the ecological effects of landscape change on wildlife (Matthiopoulos et al. 2011).

In this chapter I explore resource selection by caracals (*Caracal caracal*) occurring within a national park surrounded by a mosaic of land uses in the city of Cape Town, South Africa. In this rapidly urbanising landscape (Turok and Borel-Saladin 2014), I test whether individuals adjust their foraging behaviour in response to modified landscape cover, thereby accommodating urban development as it becomes more prevalent in their foraging range. Caracals are elusive, medium-sized felids with a diverse prey base across their geographic range (Avenant and Nel 2002; Drouilly et al. 2019; Chapter 2). In Cape Town they are the largest remaining indigenous predator and hunt largely within 200 m of urban areas. Synanthropic (i.e., human-associated) prey forms over half of consumed prey biomass (Leighton et al. 2020; Chapter 2), suggesting that caracals may selectively forage at the resource-rich urban edge, despite associated risks (Serieys et al. 2019) and high mortality. The primary lethal threats to caracals in this study system (that account for > 82% of mortalities, n = 90; L. Serieys*, unpubl. data*) are vehicle collisions, poaching, lethal management as damage-causing animals, and domestic dog attacks, demonstrating that risk associated with human activities is real. Here I first use resource selection models to determine the effect of anthropogenic and natural landscape features on caracal foraging and resting behaviour, with the expectation that selection will vary relative to their local established environments (primarily urban or wildland areas). I then test whether caracals mitigate risk of detection when foraging in urban areas by exploiting temporal or spatial refugia, including the adjusted timing of foraging and prey handling. Finally, I assess whether foraging close to the urban edge improves individual caracal body condition through increased access to prey resources. I discuss my findings within the framework of how flexible behavioural strategies may influence species persistence in ostensibly sub-optimal urban habitats and the possible consequences of foraging at the urban edge.

MATERIALS AND METHODS

STUDY AREA

I investigated foraging and resting habitat selection across the Cape Peninsula (hereafter "Peninsula"), a fragmented mosaic of predominantly wildland habitat which together forms the Table Mountain National Park (TMNP; 320 km^2). Caracal density estimates vary considerably across South Africa (0.15 – 0.47

caracals/km^2), meaning the Peninsula (~ 320 km^2 available wildlife habitat) population size could be between 48 to 150 individuals (Avenant et al. 2016). The Peninsula is geographically isolated by 2,445 km^2 of dense urban development within the city of Cape Town (Fig. 3.1A). TMNP receives on average 4.2 million visitors annually (sanparks.org) and recreational activities are permitted (e.g., walking domestic dogs and hiking) but with restrictions on such activities in the southern reserve section. The TMNP borders shift from predominantly urban in the north (Fig. 3.1A; 187 km^2 available wildlife habitat, 78% bordered by urban development) to more wildland habitat in the south (133 km^2 available wildlife habitat, 46% bordered by urban development). I explored resource selection based on two categories of land cover: urban and wildland (i.e., predominantly indigenous vegetation including formally protected areas and undeveloped land). I therefore divided the study area (Fig. 3.1; Table 3.1): urban-dominated in the north (hereafter "urban region") versus wildland-dominated in the south (hereafter "wildland region").

Protected areas with the study area are predominantly endangered Peninsula Sandstone fynbos, a dense shrubland providing medium – high cover. Land-use includes residential, light industrial, cultivated (pine plantations and commercial vineyards; Fig. 3.1A), and altered-open areas (e.g., sports fields, golf courses and greenbelts).

CARACAL CAPTURE AND COLLARING

As outlined in Chapter 2, between 2014 – 2016, 26 caracals were captured in cage traps and GPS-collared (Followit^{TM} Tellus, Lindesberg, Sweden), including one relocated female. Collars recorded at two fix intervals for a maximum of six months: every three hours, and every 20-minutes for 24 – 36 hours on every 9 – 10th day. Animal capture, handling, and sampling protocols followed ethical guidelines and permits (see Chapter 1 for details).

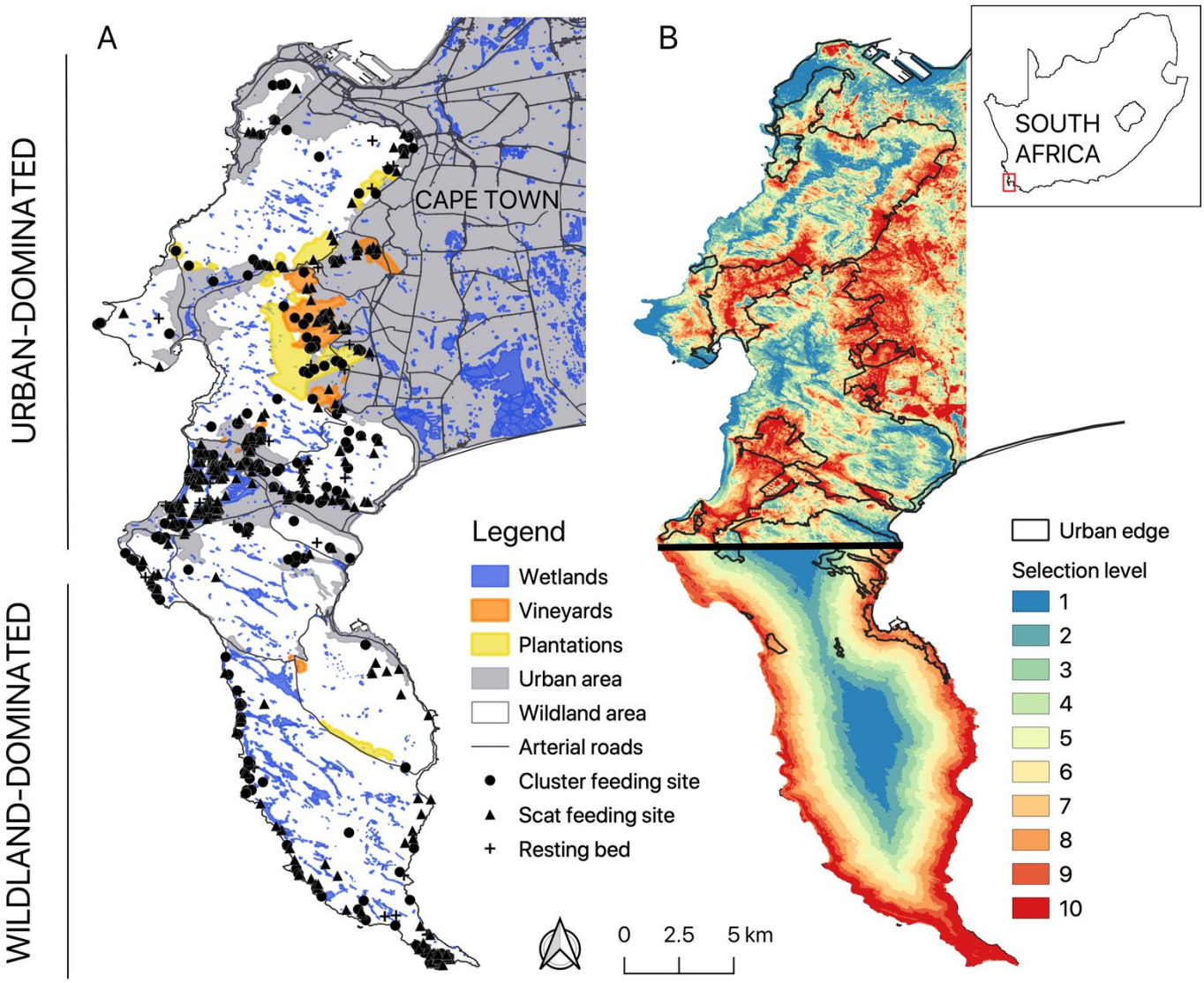


Fig. 3.1 Cape Peninsula study area showing (**A**) feeding clusters (circles, n = 326), back-traced scats feeding events (triangles, n = 384) and resting beds (crosses, n = 117), and (**B**) selection surface for urban-dominated and wildland-dominated regions with estimates based on the top land-use integrated-diet (scaled) RSF models. Higher values indicate stronger positive selection.

Table 3.1 Summary of movement, foraging and resting site data for collared caracals (n = 17) on the Cape Peninsula, South Africa (*mean ± SD*). The relocated female was removed from the wildland-dominated to the urban-dominated region.

Region	Sex	Age	n	Days tracked	Home range area (km^2)	Proportion urban area	GPS cluster prey remains (n = 326)	Scat prey remains (n = 377)	Resting beds (n = 117)
Urban-dominated	female	adult	3	185.67 ± 96.67	14.04 ± 4.04	0.11 ± 0.05	18.00 ± 10.39	23.33 ± 17.90	8.00 ± 6.00
		subadult	1	185.00	7.57	0.03	15.00	38.00	2.00
	male	adult	5	201.80 ± 68.29	72.89 ± 24.34	0.20 ± 0.09	19.40 ± 14.79	22.40 ± 18.72	6.20 ± 4.09
		subadult	4	146.67 ± 29.47	54.43 ± 36.59	0.27 ± 0.02	17.75 ± 1.12	17.75 ± 13.20	7.75 ± 3.50
Wildland-dominated	female	adult	2	138.75 ± 155.56	32.06 ± 22.68	0.01 ± 0.01	24.00 ± 28.28	16.00 ± 22.63	2.00 ± 1.41
	male	adult	1	301.00	111.00	0.01	34.00	47.00	8.00
Relocated	female	adult	1	131.00	7.85	0.02	7.00	7.00	4.00

FORAGING DATASETS

Peninsula caracal diet was previously assessed (Chapter 2) by identifying and quantifying prey remains based on i) at GPS-clusters (hereafter "feeding clusters"); ii) in scat found at GPS-clusters; and iii) the integration of the clusters and scat to account for "missed" feeding events (i.e., the "integrated-diet" approach; Leighton et al. 2020).

GPS-clusters and scat

As described in Chapter 2, I applied a Python algorithm (Python Software Foundation; Knopff et al. 2009) to identify feeding clusters that informed medium- to large-sized prey kills and resting sites from individual movement data. On-the-ground investigations of GPS-clusters were conducted and a 50 m radius (Svoboda et al. 2013) was searched for prey remains, scat, and resting beds. To quantify degree of vegetative cover, canopy density was measured (0 – 100%) using a densiometer (Forestry Suppliers, Inc., Jackson, USA) at the site of the prey remains or, when there were no prey remains detected, at the cluster centroid. Five measurements were taken (at the kill site and one metre from it in each cardinal direction) and averaged. I then categorised this *in situ* measure of degree of cover into low (0 – 33%), medium (33 – 67%) and high (67 – 100%) cover classes. Feeding cluster remains were biased towards birds (as discarded feathers are easy to detect), whereas scat prey remains were typically small species (< 0.11 kg) that a caracal could consume over a duration too short for a GPS-cluster to form (Chapter 2).

Scat samples, which informed small- to medium-sized prey, were collected at GPS-clusters. Prey found in scat at feeding clusters rarely matched (6.09%) the unconsumed prey remains, indicating that my scat dataset largely represented "missed" GPS cluster feeding events (i.e., inconsistent with prey remains identified at either the current cluster or a previous cluster) that occurred between clustering events that were detected and visited. Using the methods described here I could not pinpoint the exact time or location that scat prey items were consumed (but see below).

Location back-tracing of scat feeding events

Foraging-explicit resource selection functions (RSFs, see below) require knowledge of all important foraging locations. However, because feeding clusters and scat-based analyses were biased, I present a third approach that incorporated both small and larger prey, using gut-transit times to "back-trace" likely foraging locations (integrated-diet approach). For each scat that likely represents a missed feeding event, I leveraged the GPS-collar data against possible gut-transit times to estimate the location closest in time to the probable feeding event time. The reference movement dataset comprised 19,005 three-hour locations, and 23,524 twenty-minute locations (2501.71 ± 1297.35 SD locations per caracal). Gut transit times depend on the size of prey consumed and can only be estimated (Jethva and Jhala 2004). I therefore used three possible transit times and assessed whether variability in digestion time altered model results. The range of digestion times was obtained from jungle cat (*Felis chaus*, of similar size to caracal) feeding trials (Chakrabarti et al. 2016). For each scat representing a missed feeding event, I back-traced the three possible locations by subtracting the three possible digestion times from the starting date and time of the GPS-cluster from which the scat originated. I then used the movement data collected (3-hour and 20-minute fixes) for each caracal to identify the location closest in time to the probable feeding event time. These back-traced locations were used in both scat-only and integrated-diet RSFs (see Table 3.4). This resulted in seven foraging datasets (Table 3.4): feeding clusters, back-traced scat feeding events (for each digestion time) and integrated-diet feeding events (for each digestion time).

Model comparisons

I first assessed the sensitivity of my approach by examining variable gut transit times including i) minimum digestion time (0.5 days), ii) maximum digestion time (4 days), and iii) a scaled measure that accounted for the mass of the prey item. The dietary datasets along with the three gut transit times were assessed quantitatively by comparing model estimates. Feeding cluster, scat-only, and integrated-diet models could result in similar estimates under two circumstances. Either i) the bias in the methods used to detect feeding events is low, so integrating datasets makes no difference to prey composition estimates and thus

foraging habitat selection, or ii) the additional prey added from other methods have similar habitat requirements to those already represented. Secondly, I tested three possible model comparison outcomes among the three digestion times: model results are i) stable because the landscape is homogenous, ii) stable because caracals are finding small prey opportunistically, indicating movement-explicit, instead of foraging-explicit habitat selection, or iii) estimates differ substantially, reflecting landscape heterogeneity and the selection of specific habitats by smaller prey on which caracals then selectively forage.

URBAN EDGE EFFECTS ON BEHAVIOUR AT FEEDING CLUSTERS

I explored whether caracals increase nocturnality and reduce handling time and feeding site fidelity in relation to proximity to the urban edge. GPS collar data indicated that individuals remained at clusters for up to six days, providing the opportunity to describe a suite of behaviours at feeding sites of medium to large-sized prey and to evaluate the effect of proximity to urban areas. Specifically, I examined: i) temporal partitioning (diel period based on local sunset and sunrise) of cluster initiation, ii) handling time (cluster duration, hours), iii) average and maximum (i.e., cluster radius) distance moved from the centroid, and iv) cluster fidelity, calculated as the inverse of the number of fixes away from the cluster over the total number of expected fixes given the cluster duration (Table 3.2). Differences between diel periods (day and night) and region (urban or wildland) were tested using linear regression for continuous dependent variables (distance and time) and quasibinomial GLMs for proportional dependent variables (fidelity and *in situ* degree of cover). Behavioural parameters were generated by the Python algorithm used to identify GPS clusters. Diel period was classified based on local sunset and sunrise times using the S*treamMetabolism* R package (Sefick 2016). I calculated lunar illumination (lux) at nocturnal clusters using the *lunar* R package (Lazaridis 2014). I excluded the relocated female in these analyses because she exhibited behaviour more similar to the caracals in the wildland-dominated region (her place of origin), and significantly altered model results.

Table 3.2 Behaviour at caracal GPS-clusters with prey remains and/or resting beds on the Cape Peninsula, South Africa (*mean ± SD*).

Region	Behaviour	Diel period	n	Duration (h)	Fidelity (%)	Radius (m)	Distance moved from centroid (m)
Urban-dominated	foraging	day	152	22.87 ± 23.51	87.95 ± 2.72	61.37 ± 36.79	28.71 ± 13.31
		night	85	24.40 ± 26.61	85.71 ± 4.01	59.99 ± 32.71	30.17 ± 13.59
	resting	day	55	21.27 ± 28.16	95.48 ± 2.97	61.37 ± 38.28	30.43 ± 15.01
		night	35	37.81 ± 45.27	87.73 ± 6.43	71.31 ± 29.24	30.04 ± 10.26
Wildland-dominated	foraging	day	23	12.82 ± 11.85	89.84 ± 6.30	52.87 ± 39.94	24.39 ± 13.63
		night	59	24.64 ± 21.93	59.11 ± 6.40	48.32 ± 29.27	30.88 ± 12.03
	resting	day	17	8.35 ± 6.70	87.40 ± 8.05	39.94 ± 26.14	27.24 ± 14.61
		night	10	21.70 ± 25.15	64.52 ± 15.13	63.50 ± 40.36	30.10 ± 9.68

HOME RANGE ESTIMATES

I assessed third-order selection, i.e., comparing used and available resources within estimated home ranges (Johnson 1980). GPS collar data collected at 3-hour intervals was used to calculate 95% LoCoH-*a* ("adaptive" Local Convex Hulls) home ranges implemented in *t-locoh* (Lyons et al. 2013). The LoCoH-*a* method incorporates space and time extracted from movement data to define isopleths (i.e., home range contour lines) that account for areas with different intensities of use (e.g., high-use: repeated foraging or resting) within a home-range (Getz et al. 2007). This method is appropriate for movement data that is influenced by irregular hard boundaries (Getz et al. 2007), such as urban and coastal edges. I started with a scaling parameter (*s*) of 0.05 followed by the multistep approach outlined by Lyons et al. (2013) to optimise parameters (i.e., number of nearest neighbours and hull-sets to choose the best *a*-value) per individual. For the relocated adult female, I calculated home range following a period of 23 days, during which time she moved from her initial relocation site to another region of the Peninsula where she remained for the duration her collar was active. She was therefore included in the urban category for resource selection models. I clipped home ranges to avoid areas of overlap with ocean. I assessed the variables influencing home range size differences across regions (urban vs. wildland, excluding the relocated female) and demographics using linear models (area) and quasibinomial GLMs suitable for proportion data (percentage urban area). All analyses were performed in R v4.0.2 (R Core Team 2020) with preloaded packages.

LANDSCAPE PREDICTOR VARIABLES

Predictor variables (Table 3.3) were grouped into the following categories that could be directly compared across urban- and wildland-dominated regions: land-use (urban, altered-open, vineyards,

plantations and wildland), vegetative cover (high or low), distance to features (arterial roads, urban edge, wetlands and coast), Landsat 8 NDVI (Normalised Difference Vegetation Index, a well-established measure of resource abundance; Pettorelli et al. 2005) and NBR2 (Normalised Burn Ratio 2, averaged over study period), elevation, slope and demographic variables (sex and age). Land-use and cover were derived from the same national landcover raster (by simplifying from 73 categories; Table 3.3). I included only main arterial roads with higher and more consistent flow of traffic to assess the relative influence of high-activity roads on caracal resource selection. For continuous covariates, I assessed autocorrelation and retained only independent variables (Pearson correlation $|r| \leq 0.53$).

Cover and land-use were non-independent ($\chi^2_4 = 1755.9$, $P < 0.001$), as they were derived from the same landcover layer. Because I was interested in caracal resource selection for both measures, separate models were run for each measure. An interaction term between cover and urban edge was also included because the importance of high cover is expected to increase with proximity to the urban edge. Cover was not included in the resting beds models for the wildland-dominated region as they only occurred in high cover. Sex and age were also non-independent ($\chi^2_1 = 62.98$, $P < 0.001$), therefore separate models were run for sex and age for caracals in the urban dominated region (where subadults were sampled; Table 3.1). Distance to urban edge was highly colinear with distance to main arterial roads ($r = 0.96$), so this latter variable was not included. Distance to urban edge and elevation were collinear, so slope (also collinear with elevation) was considered in all full models. Additionally, NDVI and NBR2 were highly correlated ($r = 0.77$), so only NDVI was included.

Table 3.3 All predictor variables considered for caracal foraging and resting habitat selection analyses on the Cape Peninsula, South Africa.

Variable	Type	Range	Source	Description
ELEVATION	Continuous	0 – 1,060.51 (m)	CoCT DEM (odp.capetown.gov.za)	10 m resolution
SLOPE	Continuous	0 – 2.73 (degrees)	CoCT (odp.capetown.gov.za)	10 m resolution
WETLANDS	Continuous	0 – 1,897.39 (m)	CoCT 2017 multipolygon (odp.capetown.gov.za)	Distance to closest pond, lake, stream or wetland
ARTERIAL ROADS	Continuous	0.01 – 3,025.32 (m)	CoCT multiline string (odp.capetown.gov.za)	Distance to closest arterial road
COAST	Continuous	0.38 – 8,209.15 (m)	CoCT polygon (odp.capetown.gov.za) updated in QGIS	Distance to coastline
URBAN EDGE	Continuous	0 – 15,564.15 (m)	CoCT polygon (web1.capetown.gov.za/web1/OpenDataPortal), manually checked and updated in QGIS	Distance to urban edge
NDVI	Continuous	-0.41 – 0.85	Landsat 8 spectral index (usgs.gov). Mean raster calculated for study period (November 2014 – October 2017)	Normalised Difference Vegetation Index. Range -1 to 1.
NBR2	Continuous	-0.04 – 0.44	Landsat 8 spectral index (usgs.gov). Mean raster calculated for study period (November 2014 – October 2017)	Normalised Burn Ratio 2. Range -1 to 1
LAND-USE	Categorical	1 – 5	South African Department of Environmental Affairs (DEA) Land-cover 2018 raster (egis.environment.gov.za/gis_data_downloads)	20m resolution. 73 categories simplified to 5 (1 = urban, 2 = altered open, 3 = vineyards, 4 = plantations, 5 = wildland areas)
COVER	Categorical	0 – 1	South African Department of Environmental Affairs (DEA) Land-cover 2018 raster (egis.environment.gov.za/gis_data_downloads)	20m resolution. 73 categories simplified to 2 (0 = low, 1 = high)
AGE	Categorical	0 – 1	This study	Adult (1) or subadult (0)
SEX	Categorical	0 – 1	This study	Male (1) or female (0)

RESOURCE SELECTION FUNCTIONS

Resource selection functions (RSFs) are spatially-explicit, predictive models of habitat selection that link landscape features and the probability of animal presence (Manly et al. 2002). I assessed caracal foraging- and resting-explicit RSFs using binomial generalised linear mixed models (GLMMs, where the binary response was observed location = 1 and available locations = 0) with "individual" as the random effect (Gillies et al. 2006) using *glmmTMB* (Brooks et al. 2017). I included a random effect term to handle the model variance between individuals, which may be especially problematic for the wildland-dominated region where sampling

was limited to three caracals (but see below for methods on RSFs testing model sensitivity to additional individuals). I estimated resource availability by sampling 20 random points within home range for each observed GPS location to obtain a 1:20 ratio of "used to available" locations. I extracted landscape variables (Table 3.3) for each available location and for each real observation classified into i) feeding clusters, ii) back-traced scat events, iii) integrated-diet events, and iv) resting beds found at GPS clusters. I ran separate models for urban and wildland-dominated regions (see Table 3.4 for the structure of the full models). I used no-intercept GLMMs with weighted available points (Muff et al. 2020) and scaled and centred covariates at the Peninsula level to facilitate direct comparison between model estimates for each region.

I selected the top model using AICc (Burnham and Anderson 2002) by fitting models with all predictor variable permutations (Table 3.4) and obtained values for the probability of selection *w* for habitat variable *x* by substituting the parameter estimates β into the exponential model and normalising:

$$w(x) = \exp(\beta_1 x_1 + \cdots + \beta_i x_i) \,/\, \max(\exp(\beta_1 x_1 + \cdots + \beta_i x_i))$$

I provide parameter estimates and 95% confidence intervals (from SE) on the logit scale (see Fig. 3.3 and Appendix 3.2 – 3.5), and plot *w*(*x*) values (see Fig. 3.3). Selection surfaces based on the best RSFs (with sex fixed to male and age fixed to adult; see Fig. 3.1B for land-use and Appendix 3.1B for cover) were created by calculating the probability of selection *w* over the rasters of used covariates with the "predict" function in R and discretising to ten equal area levels of selection (Morris et al. 2016) before plotting in QGIS (version 3.2.1-Bonn; QGIS Development Team 2020).

To further validate my results in the wildland-dominated region where only three individuals were collared, I compared RSF models with and without additional individuals which also created clusters, but which were not investigated due to logistical constraints. For this analysis, I tested model estimate sensitivity to additional individuals by assessing change in coefficient estimates when running GLMMs using all generated cluster centroids (i.e., the centre GPS location for both clusters that were investigated and those that were not). These generated clusters represent any time a caracal paused on the landscape for more than three hours, including both feeding and resting events. I compared estimate values for models with the original three individuals for which I had feeding events (n = 1,398 cluster locations), and for models with five individuals (including two additional individuals for which I had cluster information, n = 1,477 cluster locations). The additional individuals were an adult female and an adult male. I ran separate models for cover and land-use variables. As in the other RSFs, I included caracal individual as a random effect.

Table 3.4 Full models considered for caracal foraging and resting habitat selection analyses on the Cape Peninsula, South Africa. Each full model was run for each dataset, resulting in 48 top models. The foraging datasets were *feeding clusters* (locations of prey remains found at GPS clusters), *scat* (prey remains in scats found at GPS clusters) and *integrated-diet* (cluster and scat prey remains combined, with duplicates removed). The digestion times for scat and integrated-diet datasets were *minimum*, *maximum,* and *scaled to prey biomass* (see *Methods*).

Region	Dataset	Predictor variable								
		Slope	NDVI	Distance to urban edge	Distance to coast	Distance to wetland	Sex	Age	Cover	Land-use
Urban-dominated	1. Feeding cluster 2. Scat: minimum	•	•	•	•	•	•		•	
	3. Scat: maximum 4. Scat: scaled	•	•	•	•	•	•			•
	5. Integrated-diet: minimum	•	•	•	•	•		•	•	
	6. Integrated-diet: maximum 7. Integrated-diet: scaled 8. Resting cluster	•	•	•	•	•		•		•
Wildland-dominated	1. Feeding cluster 2. Scat: minimum	•	•	•	•	•	•	NA	•	
	3. Scat: maximum 4. Scat: scaled									
	5. Integrated-diet: minimum 6. Integrated-diet: maximum 7. Integrated-diet: scaled 8. Resting cluster	•	•	•	•	•	•	NA		•

BODY CONDITION INDEX

The influence of home range characteristics (size and proportion urban area) on individual body condition of Peninsula caracal was also investigated. Body Condition Index (BCI) was calculated by regressing body length (mm) against animal weight (kg) to obtain ordinary least squares (OLS) residuals (n = 38 capture; n = 17 opportunistically collected intact roadkill individuals), as validated in other carnivores (Labocha et al. 2014). Body measurement trends differed significantly between sexes ($F_{2,49} = 17.66$, $p < 0.001$) and ages ($F_{2,49} = 11.15$, $p < 0.001$). Therefore, OLS residuals were calculated separately for adult males, adult females, subadult males, and subadult females. Residuals were scaled to obtain a bounded BCI (0 – poor to 1 – good). I tested BCI (response variable) against home range area and percentage urban area in home range using GLMs.

FUNCTIONAL RESPONSES TO THE URBAN EDGE

Functional responses can reveal trade-offs between mortality risk and foraging success. To investigate this in caracals, I tested whether the distance of foraging sites to the urban edge varies as a function of its availability (i.e., availability of the urban edge). I calculated a resource-selection proportion per individual by dividing the mean distance to the urban edge at used locations by the sum of the mean distance at used and available locations within the home range (i.e., mean used distance / [mean used + mean available]) following Benson et al. (2016). I explored potential functional responses by modelling these resource-selection proportions (as the response variable) as a function of distance-based resource availability of the same resource (as the predictor variable, i.e., the mean distance to the urban edge across home ranges) using quasibinomial GLMs which are appropriate for conducting regression on a proportional response variable. I performed GLMs with and without the relocated adult female and found her functional response was influenced by her place of origin. I therefore excluded her from the final analysis.

RESULTS

Of the 26 individuals GPS-collared between November 2014 and September 2016, resource selection was assessed for 17 individuals (≥ 1 month of movement data and ≥ 2 GPS cluster prey remains; $n_{urban} = 14$, $n_{wildland} = 3$; Table 3.1). Individuals were monitored for a mean of 154 ± 96.7 SD days (Table 3.1). One adult female was relocated (TMC27; Table 3.1) by the City of Cape Town from the wildland region (Simon's Town on the south-eastern coastline of the Peninsula), where she was predating on Endangered (EN; BirdLife International 2020) African penguins (*Spheniscus demersus*), to the urban region (Orangekloof in TMNP). Five individuals were opportunistically re-collared. One subadult male individual was recollared as an adult. I calculated two home ranges for these two collaring events and considered them two "individuals", thus including a total of 17 individuals.

FORAGING AND RESTING SITE SAMPLING

In total, 677 GPS-clusters were investigated, and I recorded 326 prey items at 241 feeding clusters. Feeding clusters had a median of one prey item detected, while 31.1% (n = 75) had ≥ 2 prey items (mean = 1.5 ± 1.19 SD kills/cluster, range = 1 – 15). A total of 654 scats were analysed, containing 913 prey items (49.0% collected at clusters). Scats contained smaller prey (mean size = 0.099 kg ± 0.078 SD) than feeding clusters (mean size = 0.98 kg ± 2.25 SD) by an order of magnitude. A total of 384 missed feeding events were detected, representing 54% of foraging events modelled using integrated-diet RSFs (total n = 710). Logistical constraints including access to sites and permit restrictions resulted in more feeding cluster events (74.8%, n

= 244; mean = 17.43 feeding clusters/individual) being sampled in the northern urban region, although more feeding events were recorded per individual in the wildland region (25.2%, n = 82; mean = 27.33 feeding clusters/individual; Table 3.1). I present findings from the wildland-dominated region but acknowledge this difference in sampling may affect the interpretation of these results (but see comparison of models with additional individuals).

Most feeding cluster prey were medium-sized birds (mass = 0.86 ± 0.52 kg). Despite similar abundance along the Peninsula coastline (Brooks and Ryan 2020), Cape cormorants (*Phalacrocorax capensis*) comprised 37% of feeding cluster detections in caracals in the wildland region, while only representing 0.9% of feeding events in the urban region (n = 5, integrated-diet). Caracals in the wildland region consume less small prey ($mean_{wildland}$ = 0.8 kg, $mean_{urban}$ = 0.4 kg, $F_{1,708}$ = 12.22, $P < 0.001$). Most scat prey items were small rodents (0.11 ± 0.08 kg). Vlei rats (*Otomys irroratus*) represented only 9% scat detections in the wildland region, while they represented 24% in urban region. These small rodent species have low digestibility (i.e., high surface area to volume ratio, Chakrabarti et al. 2016). Therefore, the mean calculated digestion time for these missed feeding events was 1 day 20 hours. A total of 117 resting beds were found at clusters (n = 90 urban, n = 27 wildland, Table 3.1), at clusters with (47%) and without (53%) detectable prey.

HOME RANGE ESTIMATES

Home range sizes were similar in both regions ($mean_{urban}$ = 48.6 ± 35.1 km^2; $mean_{wildland}$ = 58.3 ± 48.1 km^2; $F_{1,14}$ = 0.16, $P = 0.69$; Table 3.1 and Fig. 3.2). Caracals in the urban region utilised more urban area ($mean_{urban}$ = 18.80% ± 9.5; $mean_{wildland}$ = 0.67% ± 0.58; β = 3.54, t = 2.20, $P < 0.05$) and female home ranges were smaller ($mean_{female}$ = 19.0 ± 14.8 km^2; $mean_{male}$ = 69.3 ± 31.7 km^2; $F_{1,14}$= 13.11, $P < 0.01$; Fig. 3.2). Males used more urban space than females ($mean_{male}$ = 20.9% ± 9.9; $mean_{female}$ = 6.3% ± 6.25; β = 1.36, t = 2.97, $P <$ 0.05), and subadults used more urban space than adults ($mean_{subadult}$ = 21.8% ± 10.6; $mean_{adult}$ = 12.5% ± 10.6; β = 0.92, t = 2.25, $P > 0.05$). While percentage of utilised urban area ranged between 0 – 33%, all caracals in this study had home ranges that abutted an urban area, with the exception of one female in the wildland region.

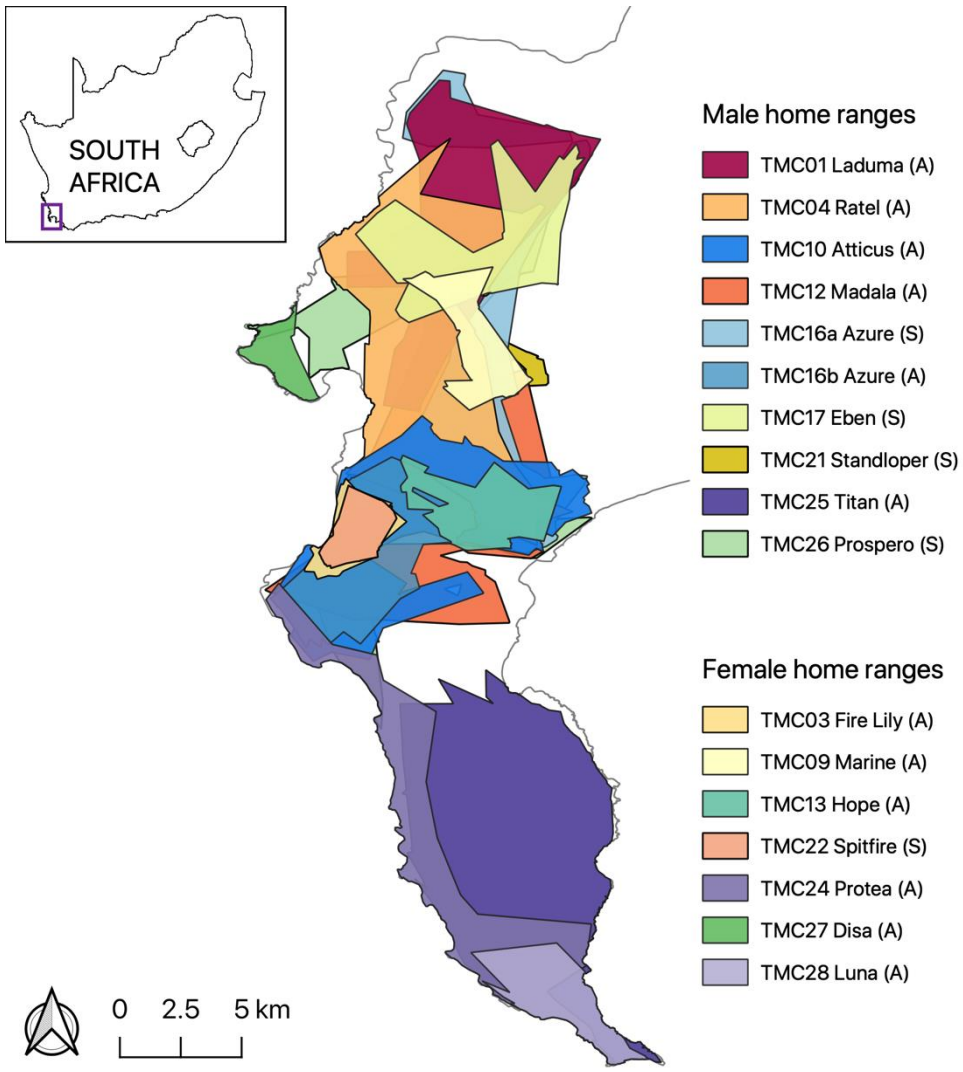


Fig. 3.2 Cape Peninsula study area showing home ranges (95% LoCoH-*a* isopleths) for adult (A) and subadult (S) male and female caracals (n = 17) considered when measuring availability (third-order selection; see *Methods*) for resource selection analysis.

Foraging habitat selection

Overall, both anthropogenic and natural landscape features influenced foraging habitat selection. Irrespective of region, gentler slopes, and greener vegetation (higher NDVI; Fig. 3.3) were selected by caracals.

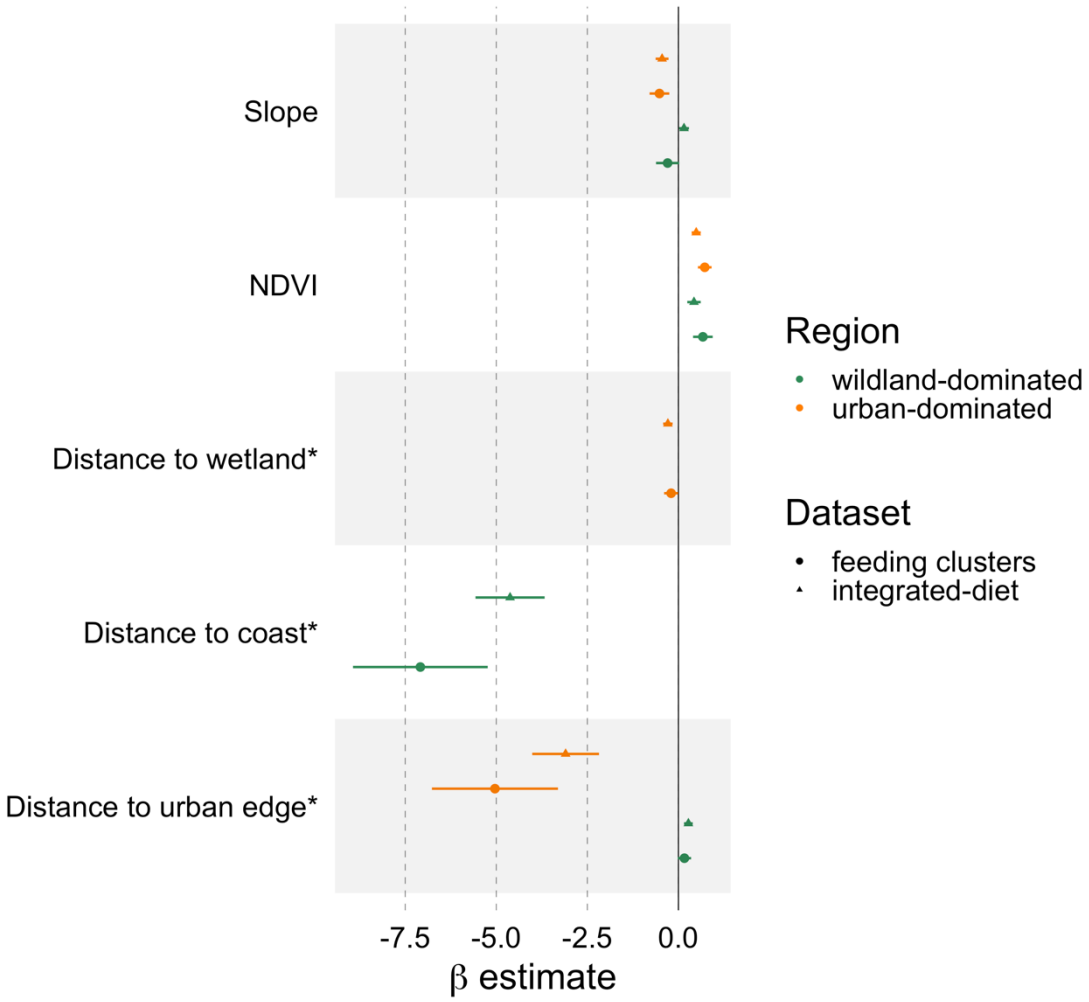


Fig. 3.3 Continuous parameter estimates and 95% confidence intervals based on standard errors for RSFs (logit scale). Estimates are shown for those parameters included in the top models (as determined by AICc) for the urban-dominated (orange) and wildland-dominated (green) regions. *Feeding clusters* (circles) is the GPS cluster prey remains dataset; *integrated-diet* (triangles) is the dataset with both cluster prey remains and scats. *Note that negative distance values indicate selection for habitat closer to the feature.

i. Inter-individual variation

Low inter-individual variation characterised caracal foraging habitat selection (variance of caracal ID random effect: urban-dominated < 0.01; *sensu* Hertel et al. 2020), even in the wildland-dominated region with few individuals (variance < 0.001). This supports results of the complimentary analyses performed in Chapter 2, showing diet composition was similar across individuals. Due to the low number of individuals in the wildland-dominated region, I tested model sensitivity to additional individuals using GPS cluster centroid locations. Estimates were very similar between these datasets (3 vs. 5 individuals) for both land-use (Appendix 3.6) and cover models (Appendix 3.7). The average change in coefficients was 0.18 for land-use models and 0.12 for cover models, and the random effect variance was low for all models (< 0.13 for land-use models and < 0.12 for cover models). While these model results do not represent foraging habitat selection, they demonstrate that estimates based on three individuals are robust and inter-individual variation remains very low even when additional individuals are included. The robust coefficient estimates suggest my results are representative of the larger subpopulation. Despite individual-level behavioural consistency within regions, I

found differences in resource selection between regions. This suggests my findings are driven by landscape differences, rather than individual behavioural variation.

ii. Urban region

Consistent across the different diet datasets (Fig. 3.1B and Fig. 3.4A), the results indicate that caracals in the urban region select to feed close to the urban edge (β = -3.1 ± 0.46; Fig. 3.3, note that negative distance values indicate selection for habitat closer to the feature). While the distance of caracal feeding events ranged from 0 – 2095 m ($median_{urban}$ = 273 m), 35.58% of feeding events were within 200 m and 58.21% were within 500 m of the urban edge. Selection for the urban edge was stronger for adults than for subadults (β_{adult} = -4.76 ± 2.94; $\beta_{juvenile}$ = -28.02 ± 3.36).

Habitat selection did, however, differ across land-use types. Although selecting for the urban edge, caracals avoided foraging within the urban matrix itself (14.4% of feeding events; β = -5.29 ± 2.95; Fig. 3.4B). Relative to availability in the landscape, caracals selected vineyards (3.5% of feeding events) and avoided plantations (2.7%), while wildland (76.1%) and altered-open (3.3%) areas were selected at similar levels (Fig 3b). In vineyards, most feeding events (64%) were within greenbelts or bushy areas alongside the trellis vines. Caracals preferred high (β = -5.33 ± 2.95; Appendix 3.4 – 3.5) to low cover (β = -2.06 ± 2.96; 88.5% high, 11.5% low). See Appendix 3.1 for the selection surface based on the top cover models. An interaction term revealed that high cover was selected closer to the urban edge, while low cover was selected further from it (β = 7.24 ± 0.67; Fig. 3.4C).

iii. Wildland region

Although limited to three individuals, caracals in this region appear to avoid the urban edge (β = 0.27 ± 0.06; Fig. 3.4A). Feeding events occurred between 106 – 15,451 m from the urban edge ($median_{wildland}$ = 10,804 m) and only 3.66% of feeding events were within 200 m of the urban edge. Rather, caracals selectively foraged on the coastline up to 15 km from urban areas (Fig. 3.1B and Fig. 3.3). Most feeding events (52.5%) were within 200 m of the coast, with a median of 180 m (mean = 299 m, range = 15 – 2870 m). Further, the overwhelming majority of caracal feeding locations were in intact, wildland areas (wildland = 97.5%, plantations = 1.23%, urban = 1.23%) with high cover (high = 74.7%, low = 25.3%). Overall, trends varied by sex with selection being significantly stronger for the male (β = -16.31 ± 0.54) than females (β = -16.75 ± 0.55; Appendix 3.2 – 3.5). The male's stronger selection for the coast may explain the dominance of seabirds in the diet (male = 64.8%, female = 20.2%) and a less diverse prey base (n_{male} = 18, n_{female} = 24 species), although this trend may be specific to this individual.

iv. Relocated caracal

Although my sample size is limited to one individual, I found further evidence suggesting that the environment (i.e., urban- vs wildland) may matter more than inherent individual differences. Among the urban group, the adult female relocated to the urban region (TMC27) was an outlier in prey preference, habitat selection, and functional response (see below). She preferred foraging along the coast, in areas with steeper slopes, and she avoided the urban edge more so than other urban individuals. She also had a lower proportion of urban area in her home range than other urban adult females (Table 3.1). Excluding her from the RSF models for the urban group marginally increased the strength of the attraction to the urban edge, showing her opposing results slightly diluted this overall trend.

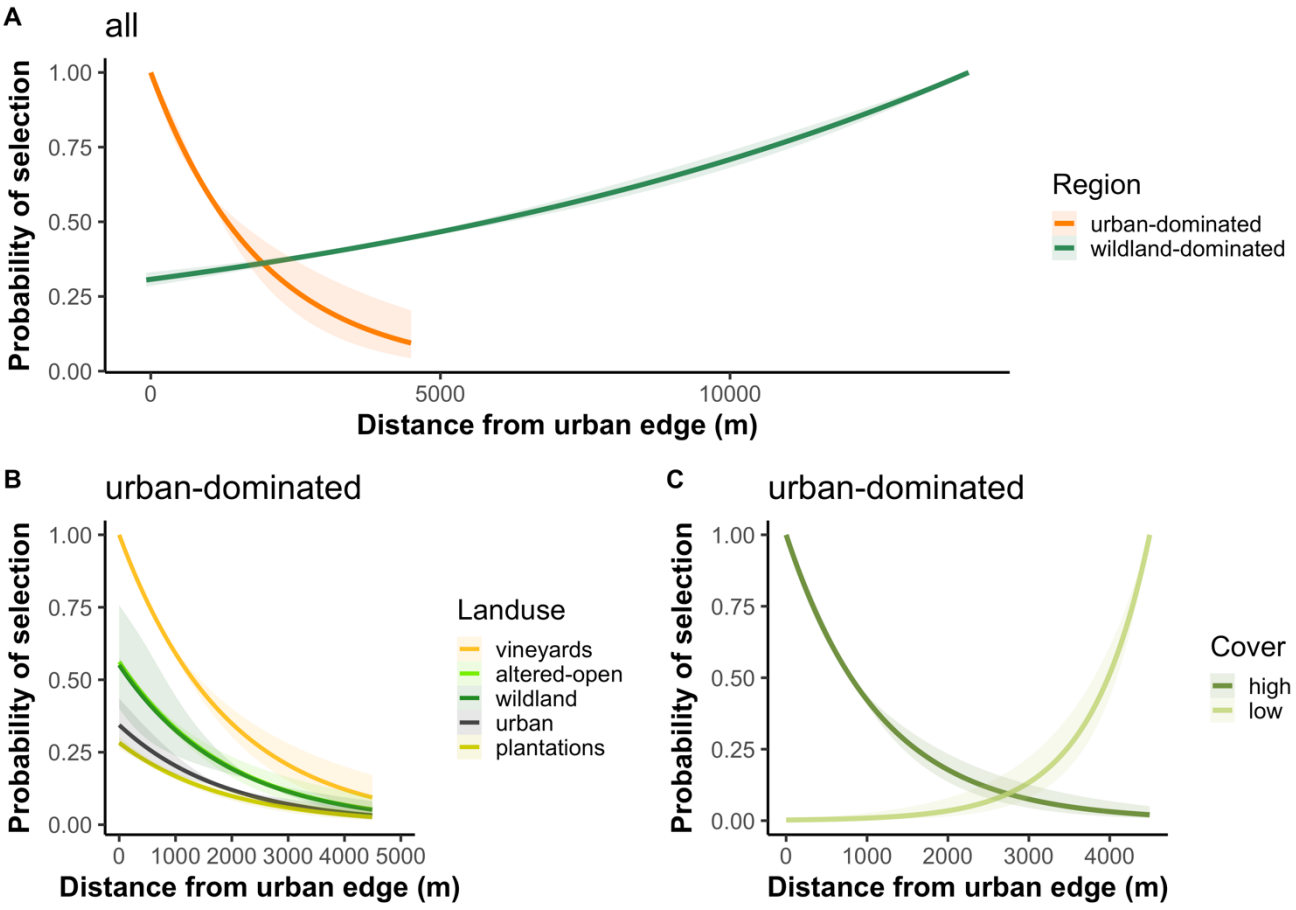


Fig. 3.4 Probability of a caracal selecting habitat given distance to the urban edge based on RSFs for, (**A**) caracals in both urban- and wildland-dominated regions and (**B**) urban-dominated region caracals for different land-uses, (**C**) at different levels of cover in the urban-dominated region for the scaled integrated-diet dataset (i.e., feeding events from both GPS cluster prey remains and scat; see *Methods*). The 95% confidence intervals are based on standard errors. Note that axes differ between plots.

Resting site selection

Caracals in both regions exhibited stronger selection for areas with greener vegetation when resting (compared to foraging), and preferred resting in areas with cover (Appendix 3.4 and 3.5). In the urban region, caracals did not choose resting sites as a function of distance to the urban edge, while caracals in the wildland region strongly avoided the urban edge when resting (Appendix 3.2 and 3.4). Models on resting sites suggested there was no effect of distance to the urban edge, wetlands, or coast in the urban region (Fig. 3.4A). Yet, notably, the urban matrix was even more strongly avoided when resting than when foraging, although the standard error was larger (Appendix 3.2).

Comparisons among feeding cluster, scat, and integrated-diet models

A novel aspect of this chapter was the use of missed feeding events (i.e., detected via scat) in foraging-explicit models. Incorporating all potential prey (integrated-diet) resulted in a more robust (lower SE) understanding of foraging-explicit habitat selection (Fig. 3.3) than when analysing feeding clusters or scat independently. Interestingly, I observed distinct trends in model optimisation when comparing region models.

For the urban region, feeding cluster and integrated-diet models were highly correlated ($r > 0.9$), with overwhelming similarity in direction and magnitude of coefficients. However, integrated-diet models did broaden resource selection estimates (i.e., moved estimates closer to zero, where zero indicates no selection). The exception was stronger selection for wetlands (Appendix 3.2 and 3.5). In the wildland region, where seabirds were the dominant prey, the integrated-diet approach added more unique prey species (particularly rodents and medium-sized mammals) and the distance to coast became less important (Fig. 3.3). Integrated-diet models also increased estimates of urban edge avoidance in caracals in the wildland region ($\beta = 0.27 \pm 0.06$).

I found inconsistencies in model results between the three digestion time methods (minimum, maximum and scaled; Appendix 3.2 and 3.5), particularly for feeding events in the wildland region. Specifically, the scaled method revealed a stronger preference for steeper slopes than the other foraging datasets ($\beta = -0.15 \pm 0.07$), while slope was dropped from the maximum digestion time model. In the models for the urban region, the discrepancies in estimates between digestion time methods were largest for NDVI and slope. Nevertheless, the overall trends revealed in the feeding cluster models were also captured by the integrated-diet approach.

Functional responses, body condition and the urban edge

Caracals exhibit a strong positive functional response to the urban edge at foraging sites. The selection for the urban edge increases with proximity to developed areas within individual home ranges (β = 0.0001, t = 2.3, $P < 0.05$; Fig. 3.5A), but especially within the urban region (β = 0.004, t = 5.7, $P < 0.001$; Fig. 3.5B). The relocated female was a clear outlier to the urban group, suggesting that foraging behaviour is maintained. There was no pattern with caracal body condition index (BCI, calculated from OLS residuals of weight and body length, n = 55) and proportion of urban area in home range (β = 1.56, t = 0.57, $P = 0.57$), or selection of urban edge based on the functional response calculation (β = -2.47, t = -1.30, $P = 0.22$). However, BCI was higher for caracals with larger home ranges (β = 0.02, t = 2.2, $P < 0.05$).

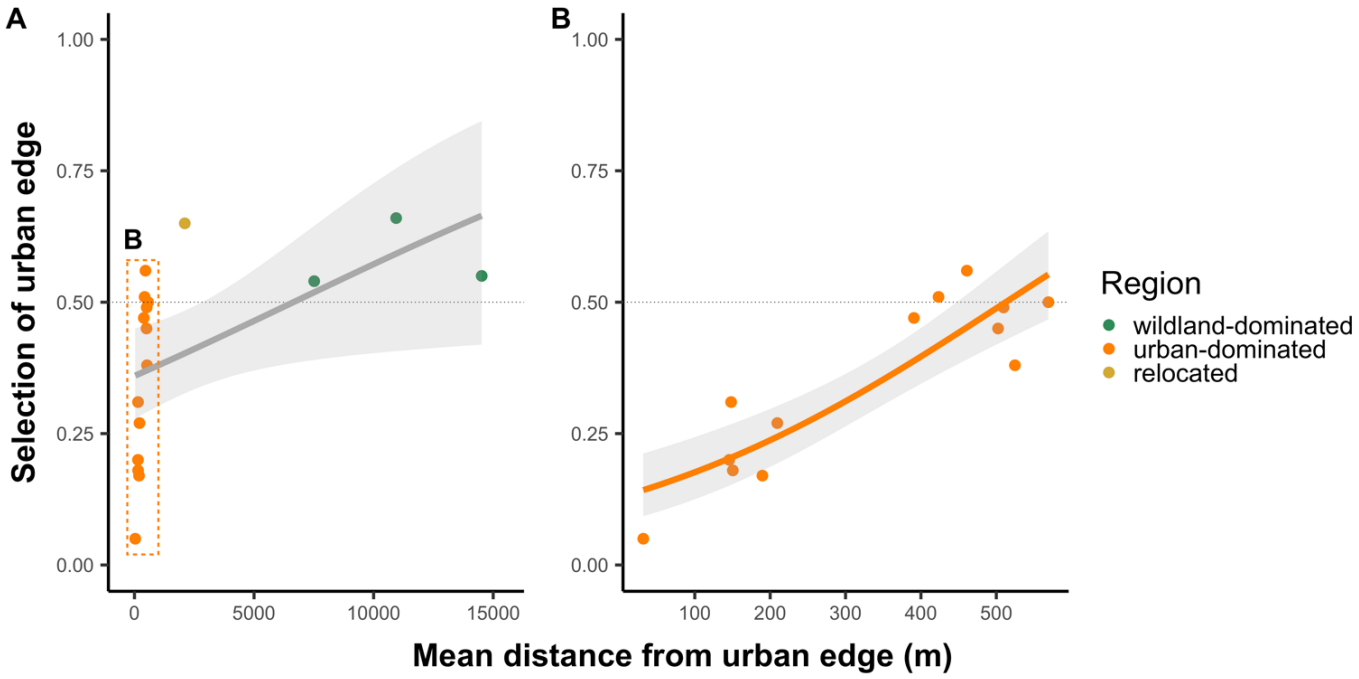


Fig 3.5. Functional response by (**A**) all caracals and (**B**) only caracals in the urban-dominated region of the Cape Peninsula, South Africa, relative to urban edge. Functional response is exhibited by the relationship between a selection proportion for the urban edge and the mean distance to the urban edge across each home range. Proportions of 0.5 represented no difference between used and available, whereas proportions < 0.5 indicated caracals were closer to the urban edge than expected, and proportions > 0.5 indicated caracals were further from the urban edge than expected.

Behavioural strategies to mitigate risk of detection

I also examined a suite of cluster characteristics to determine if caracals in urban and wildland regions employ different tactics to mitigate detection risk when foraging at the urban edge.

i. Diel period

Unexpectedly, individuals in the urban region initiated the majority (63.1%) of feeding clusters during the day ($\chi^2_1 = 16.79$, $P < 0.001$, Table 3.2). To ensure that the feeding clusters investigated (as opposed to all those generated) were not biased towards one diel period, I calculated that 57% of all generated clusters were formed during the day. When accounting for small prey feeding events (i.e., integrated-diet), the trend was stable (diurnal = 61.1%; nocturnal = 38.9%). In contrast, only 28.0% of caracal feeding clusters in the wildland region were initiated during the day, with 72.0% initiated at night ($\chi^2_1 = 15.81$, $P < 0.001$; Table 3.2). Unlike individuals in the urban region, when incorporating small prey, caracal kills in the wildland region were more evenly spread over diel periods (diurnal = 46.9%, nocturnal = 53.1%).

ii. Distance to the urban edge

Diurnal feeding clusters were closer to the urban edge ($mean_{diurnal} = 240$ m, range = 0 – 2,010 m; $mean_{nocturnal} = 333$ m, range = 0 – 2,095 m; $F_{1,235} = 3.88$, $P = 0.05$) for caracals in the urban region. To compare between regions, I filtered points to < 5 km from the urban edge (maximum distance in the urban region). In contrast, diurnal feeding clusters in the wildland region were further from the urban edge (mean = 3,412 m, range = 1953 – 4580 m), with nocturnal kills being closer on average (mean = 2,088 m, range = 106 – 4,538 m), although the difference was only marginally significant ($F_{1,19} = 3.3$, $P = 0.08$). Lunar illumination was not associated with the distance of nocturnal feeding clusters from the urban edge (urban: $F_{1,83} = 1.75$, $P = 0.19$; wildland: $F_{1,15} = 0.99$, $P = 0.33$).

iii. Degree of in situ *vegetation cover*

As the distance from urban edge decreased, the degree of cover (0 – 100%, measured *in situ* at clusters) at feeding clusters increased ($\beta = -0.0001$, $t = -6.37$, $P < 0.001$; Fig. 3.6A). Further, the average feeding cluster in the urban region had a greater degree of cover (mean = 69.1%) than the average cluster in the wildland region (46.1%; $\beta = -0.96$, $t = -3.63$, $P < 0.001$). Caracals predominantly established feeding clusters in areas with higher cover during the day ($mean_{day} = 75.8\%$; $mean_{night} = 45.4\%$, $\beta = -1.25$, $t = -5.88$, $P < 0.001$; Fig. 3.6A).

iv. Handling time

Caracals in both regions spent similar amounts of time at feeding clusters (mean = 23.3 hours, range = 1 – 141 hours; $F_{1,317} = 0.76$, $P = 0.38$; Table 3.2). However, handling time during the day was almost twice as long for caracals in the urban region ($F_{1,173} = 4.63$, $P < 0.05$; Table 3.2). The patterns were stable when controlling for prey type: considering only diurnal feeding clusters with medium-sized bird remains, I found handling time during the day was almost twice as long for caracals in the urban-dominated region ($F_{1,100} = 3.94$, $P < 0.05$).

Caracals in the urban region exhibited similar handling times during the day (mean = 23.8 hours) and night (24.4 hours; $F_1 = 0.03$, $P = 0.86$), regardless of distance from the urban edge (up to 2,095 m from the urban edge; $F_{1,235} = 0.95$, $P = 0.33$). In contrast, with increasing proximity to urban areas, feeding clusters of caracals in the wildland region had longer handling time ($F_{1,80} = 12.19$, $P < 0.001$; Fig. 3.6B). Diel period and degree of cover significantly affected caracal handling time in the wildland region ($F_{2,79} = 8.36$, $P < 0.001$), but had no effect on caracals in the urban region ($F_{3,215} = 0.58$, $P = 0.63$). Handling time at diurnal feeding clusters in the wildland region was, on average, twice as long when in high cover areas ($mean_{high} = 15.7$ hours; $mean_{low} = 7.4$ hours; $F_{2,79} = 8.36$, $P < 0.001$). In the wildland region nocturnal clusters were longer than diurnal ones, particularly when in high cover ($mean_{high} = 34$ hours; $mean_{low} = 18.6$ hours; $F_{2,79} = 8.36$, $P < 0.001$; Fig. 3.6B). I found there were no significant sex differences in handling time for caracals in the urban-dominated ($F_{2,234} = 0.16$, $P = 0.69$) or wildland-dominated region ($F_{2,80} = 0.27$, $P = 0.61$). Furthermore, nocturnal handling time was not affected by lunar illumination in urban-dominated ($F_{1,83} = 2.58$, $P = 0.11$) nor wildland-dominated regions ($F_{1,57} = 0.11$, $P = 0.74$).

v. Fidelity

Longer handling times with increasing proximity to the urban edge may reflect individuals seeking spatial refuge away from clusters when not actively feeding. Therefore, I examined fidelity to feeding clusters. Overall, caracals in the wildland region had lower fidelity ($mean_{wildland} = 67.7\%$) than caracals in the urban region ($mean_{urban} = 87.2\%$; $\beta = 1.18$, $t = 5.21$, $P < 0.001$), particularly at night ($\beta = -1.43$, $t = -4.60$, $P < 0.001$; Table 3.2). In the urban region fidelity was not related to diel period ($\beta = -0.19$, $t = -0.68$, $P = 0.50$) or degree of cover ($p > 0.05$). In contrast, caracals in the wildland region had 30.7% higher fidelity during the day than a night ($mean_{day} = 89.8\%$; $mean_{night} = 59.1\%$; $\beta = 0.60$, $t = -3.0$, $P < 0.01$; Fig. 3.6C). Fidelity in the urban region remained very high (≥ 80%) in all cases (up to 2,095 m from the urban edge). There was no influence of urban edge distance in this region ($\beta = 0.0005$, $t = 0.92$, $P = 0.36$). In contrast, caracals in the wildland region had higher fidelity when closer to the urban edge ($\beta = -0.0001$, $t = -2.51$, $P < 0.05$), particularly at night ($\beta = -1.81$, $t = -3.03$, $P < 0.01$). During the day, fidelity was high across all distances from the urban edge (Fig. 3.6C). Further, when cover was high, fidelity increased ($\beta = 1.38$, $z = 2.63$, $P < 0.01$). There were no sex differences in cluster fidelity for caracals in the urban-dominated region ($\beta = 0.51$, $t = 1.80$, $P = 0.07$). However, there were strongly significant sex differences in fidelity for caracals in the wildland-dominated region ($\beta = -1.83$, $t = -4.35$, $P < 0.001$): the male had much lower fidelity than the females. There was no effect of lunar illumination on fidelity for nocturnal clusters in the urban region ($\beta = -0.03$, $t = -0.05$, $P = 0.95$). In the wildland region nocturnal clusters had significantly lower fidelity when lunar illumination was high ($\beta = -1.86$, $t = -2.46$, $P < 0.05$).

When fidelity was low there was little pattern seen with distance moved from feeding cluster centroid and distance to urban edge between day and night for caracals in the urban-dominated region (overall mean

= 28.3m; $F_{1,1} = 0.32$, $P = 0.57$), while caracals in the wildland-dominated region moved further from the centroid at night (mean = 30.9 m) than in the day (mean = 24.4 m; $F_{1,1} = 5.34$, $P < 0.05$; Table 3.2).

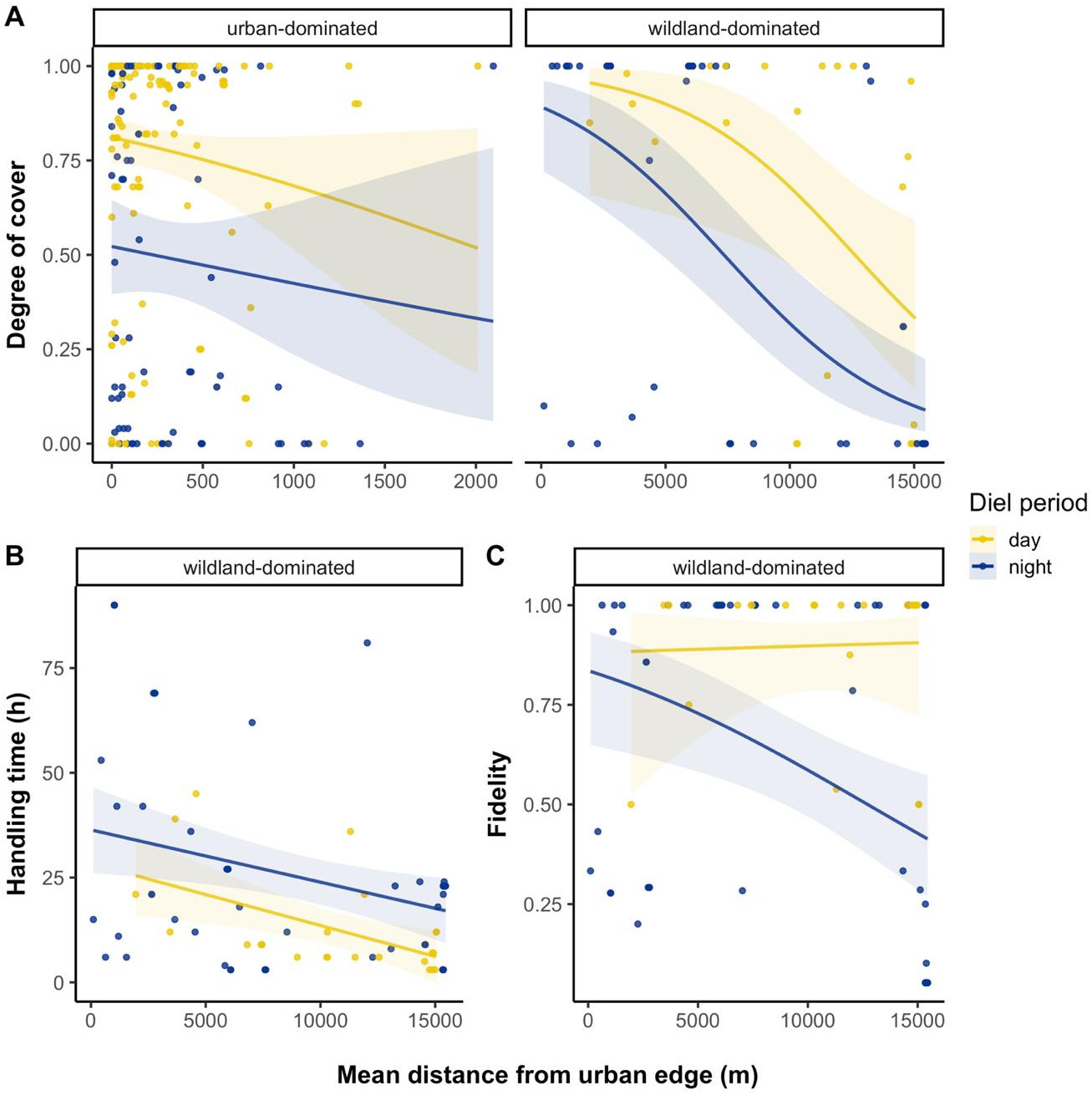


Fig. 3.6 Caracal feeding cluster variables against distance from the urban edge between diel periods: (**A**) degree of cover measured *in situ* at clusters (**B**) handling time in the wildland-dominated region (**C**) cluster fidelity in the wildland-dominated region of the Cape Peninsula, South Africa. Note that axes differ between plots.

DISCUSSION

In this chapter I explored caracal foraging behaviour across a gradient of urbanisation and present a novel data approach that incorporates a suite of diverse prey feeding locations into resource selection analysis. Level of exposure to urbanisation influenced individual foraging behaviour, with low interindividual variation but marked differences between urban and wildland regions. Caracals living in the urban-dominated northern region adjacent to the city of Cape Town select to forage close to the urban edge. Here they develop unique strategies to mitigate risk: opting to "hide in plain sight" (i.e., staying unnoticed in a setting that masks presence) to avoid detection, rather than spatial or temporal partitioning to avoid human-associated risk altogether. This strategy may lend caracals, and potentially other carnivores that adopt similar strategies, greater foraging opportunities and therefore resilience in increasingly urbanising areas; however, it carries a suite of associated risks that may jeopardise long-term persistence.

THE INTEGRATED-DIET APPROACH REVEALS UNIQUE INSIGHTS INTO HABITAT SELECTION

The results presented here suggest that caracals in the urban-dominated region selectively forage close to the urban edge, despite disturbances that may be perceived as risky, such as the presence of hikers, park rangers, as well as deadly threats such as vehicles (> 72% of deaths), poachers (7%), and domestic dogs (3%). In assessing foraging habitat selection that may be used in downstream management for generalist, urban-tolerant mesocarnivores, it is critical that the full suite of foraging events is included in RSF analyses. As for other carnivores (e.g., Bacon et al. 2011; Tambling et al. 2012; Pitman et al. 2014; Perilli et al. 2016; Studd et al. 2021), I have found that scat analysis overestimates smaller prey, while GPS cluster analysis overestimates larger prey (Chapter 2; Leighton et al. 2020), highlighting the need to integrate these methods, particularly for smaller carnivores that feed across a range of prey sizes. Importantly, integrated-diet data clearly improves model resolution, particularly with respect to the relative importance of natural and anthropogenic landscape features. For instance, in the urban region distance to wetlands was more important for foraging and the urban edge was less strongly selected when smaller prey were incorporated. This I attribute to the inclusion of vlei rats (*Otomys irroratus*, wetland habitat specialists; Curtis and Perrin 1979), which were only represented in scat sampling. In the wildland region, integrating diet datasets added prey species other than seabirds, reducing the strength of selection for the coast. Additionally, this novel approach revealed selection for steeper slopes. This is perhaps due to the inclusion of hyrax (*Procavia capensis*), a medium-sized mammal inhabiting rocky outcrops and cliffs (Kotler et al. 1999), also only recorded in scats. This suggests selection of particular mammalian prey habitat patches that would be missed by cluster analysis alone, and that using digestion time scaled to prey mass is likely the most appropriate integrated-diet method for RSFs in medium-sized carnivores.

FUNCTIONAL RESPONSE AND SELECTION OF THE URBAN EDGE

The positive functional response to the urban edge reveals that caracals modify their foraging habitat-selection patterns depending on the landscape in which they find themselves. Specifically, caracals, particularly in the urban-dominated region, selected for the urban edge more when it was more prevalent on the landscape, as documented in carnivores for other urban features (e.g., pumas and wolves, *Canis lupus*; Mckenzie et al. 2012; Knopff et al. 2014; Zimmermann et al. 2014). Selection of the urban edge was dependant on land-use and not all transformed areas were selected equally. While commercial pine plantations do not apparently provide adequate resources, cultivated vineyard properties were strongly selected, as they likely provide higher prey availability. Additionally, unlike plantations, vineyards provide patches of closed cover between and alongside vines not often frequented by people, where most feeding events were located. Retaining adequate greenbelts may therefore facilitate caracal foraging. Yet there may be hidden risks to foraging in vineyards. Caracal proximity to vineyards was significantly associated with anticoagulant rodenticide exposure, which was implicated in the death of at least two study animals (Serieys et al. 2019).

Caracals in the urban region, like other felids (Riley et al. 2003; Athreya et al. 2013; Bista et al. 2020), generally mitigate risk by avoiding the urban matrix, remaining on the periphery. Attraction to the urban edge is likely due to greater resource availability as a product of lower elevation and added resource input through human activities (Fleming and Bateman 2018). In my study area, development is concentrated in low-lying areas with productive soils (Rebelo et al. 2011), while intact wildland areas predominantly comprise high lying, nutrient-poor fynbos vegetation and few palatable grasses for prey (van Hensbergen et al. 1992). Habitat disturbance at the urban edge, such as frequent anthropogenic fires (Forsyth and Van Wilgen 2008), alien clearing and maintenance of fire breaks, greenbelts and golf courses may increase secondary succession grasses (Milton 2004; Yelenik et al. 2004; Reinecke et al. 2008), which are favourable habitat for select prey, principally vlei rats, striped mice, and Egyptian geese (MacKay et al. 2014). While local prey distribution data is limited, commonly consumed avian prey are more abundant at the urban edge (e.g., pigeons, *Columba livia*, and Guinea fowl, Suri et al. 2017). However, I did not find an association between use of urban areas and increased body condition, although this may be due to limitations of the scoring method and sample size (Peig and Green 2009).

Although subadults had proportionally more urban area in their home ranges compared to adults, they showed weaker selection for the urban edge relative to its availability. This may be due to competitive exclusion by larger, older conspecifics favouring the urban edge but avoiding the urban matrix. At least two subadults on the Peninsula died due to conspecific aggression (Serieys, *unpubl. data*) revealing strong competition for resources. Similar results have been documented in peri-urban populations of bobcats and pumas (Riley et al. 2003; Benson et al. 2020). The mortality risk from adults is likely exacerbated in this population, where dispersal by subadults is restricted by the dense urban matrix. These results suggest that

while optimal foraging may be focused at the urban edge, there is likely intense competition between individuals causing younger, less competitive individuals to forage further into urban areas.

HABITUATION TO HUMAN DISTURBANCE AND HUMAN DETECTION RISK MITIGATION

Carnivore success in transformed landscapes is increasingly linked to their ability to either avoid or accommodate human activities through flexible behaviour (Knopff et al. 2014; Suraci et al. 2019b). The human apex predator creates disturbance stimuli that can have far-reaching spatial effects (Andersen and Aars 2008; Suraci et al. 2019b). While feeding, the perceived presence of predators can likewise lead to shifts in behaviour: large carnivores reduce handling times and flee more frequently in response to anthropogenic disturbance (Kerley et al. 2002; Smith et al. 2017). I compared foraging behaviour in regions with differing levels of anthropogenic risk, and despite the low number of individuals in the wildland-dominated region, these results provide a valuable baseline expectation. However, I acknowledge that these trends could be specific to these individuals and therefore focus my interpretation on the caracals in the urban-dominated region. I found that when in urban-dominated landscapes during the day, caracal handling time and fidelity to clusters was greater compared with those of caracals in the wildland region. Remarkably, caracals in the urban region had consistently high fidelity (> 80%) to feeding sites and similar handling times, suggesting that they perceived similar risk regardless of diel period or distance from the urban edge. Contrastingly, caracals less exposed to urbanisation appear to mediate behaviour based on perceived human detection risk: at night, when risk of detection is lower, is the only time they forage close (< 1 km) to the urban edge, and it is only when close to the urban edge that they remain hidden (i.e., leave feeding sites less and extend handling time). The continued avoidance of the urban edge by the relocated female suggests that foraging behaviour is maintained, or at least there is initial inertia in behaviour, despite the influence of a new, more urbanised environment. The lack of spatial avoidance by caracals in urban- compared to wildland-dominated areas points to behavioural plasticity and habituation to human presence, likely due to frequent exposure to non-lethal encounters (Wheat and Wilmers 2016; Schell et al. 2018).

In urbanised areas with few green spaces, species may be expected to use temporal avoidance of humans to lower their risk (Gaynor et al. 2018). However, in the urban region temporal patterns in caracal foraging appear to strictly track prey activity (> 60% diurnal clusters), corroborating recent evidence that medium-sized carnivores do not always increase nocturnality (Frey et al. 2020). While the trend was unexpected, the most important caracal prey items in the urban region are more active during daylight: vlei rats are mainly crepuscular, and Guinea fowl and striped grass mice are diurnal. In contrast, in the wildland region, more feeding events were nocturnal (> 50%). Here the dominant prey, cormorants, are diurnal but regularly forage 10 – 20 km offshore (Ryan et al. 2010; Hamann et al. 2012) while at night, they roost in large coastal colonies, where they may are more vulnerable to terrestrial predators. Thus, caracal foraging activity

appears to be dictated by optimal hunting success (Avenant and Nel 2002), and not temporal avoidance of the human apex predator.

In lieu of temporal or spatial refugia, caracals in the urban region reduce movement and make use of vegetative cover to "hide in plain sight" in high-quality patches. When the human apex predator appears on the landscape, the most effective predator-avoidance tactic may be to remain stationary, although this is traditionally attributed to herbivore prey species (Broom and Ruxton 2005; Laundré 2010). I observe that, like other carnivores (e.g., hyenas, Boydston et al. 2003; brown bears, Ordiz et al. 2011; wolves, Llaneza et al. 2016; Eurasian lynx, Bouyer et al. 2015b; Belotti et al. 2018; Hočevar et al. 2021), caracals select high cover to improve concealment when foraging and resting at the urban edge, relying on their reddish-brown coat for camouflage (Sunquist and Sunquist 2002). Additionally, as an ambush predator, selection of higher cover may also improve ability to stalk prey (Smith et al. 2020a). The availability of dense fynbos, or natural vegetation patches in and around trellis vineyards and greenbelts, lends success to this strategy as urbanisation expands. Remaining hidden could also have energetic benefits. Caracals move off kills less and therefore do not have to increase their kill rate (Smith et al. 2015; Belotti et al. 2018) or increase the duration or intensity of movement (Ordiz et al. 2014; Oriol-Cotterill et al. 2015a). However, long periods spent at the urban edge may increase competition with other species that may be capitalising on urban resources (e.g., large-spotted genet, *Genetta tigrina*; Widdows and Downs 2015, 2016) or increase exposure to anthropogenic threats (e.g., poachers and domestic dogs).

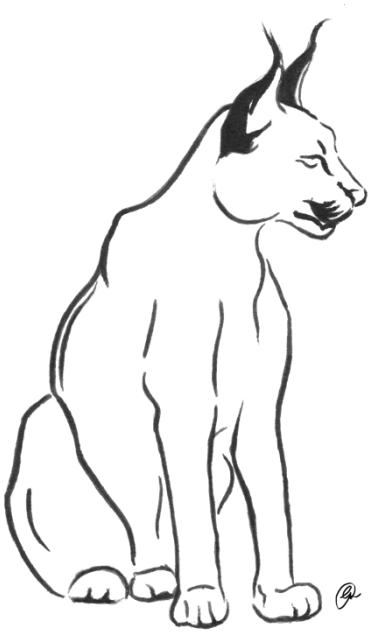
MANAGEMENT IMPLICATIONS AND CONCLUSIONS

Foraging at the urban edge is likely to have numerous adverse consequences, even when wildlife employ ecologically adaptive risk-avoidance strategies. Dense road systems are a major cause of wildlife mortality (Seiler and Helldin 2006; Hill et al. 2020b), particularly for Cape Town's caracals (Serieys et al., *unpubl. data*) and peri-urban mesocarnivores globally (e.g., Poessel et al. 2014; Litvaitis et al. 2015; Garrote et al. 2018; Serieys et al. 2021). As for other medium-sized felids (e.g., Riley et al. 2004; Mateo et al. 2012; Serieys et al. 2015; Boyles and Nielsen 2017), exposure to pollutants (e.g. rodenticides, Serieys et al. 2019; Chapter 4) and diseases (10% of deaths; Serieys, *unpubl. data*) that are uniquely associated with human-modified areas may also exacerbate risks (Murray et al. 2019). Despite the low incidence of caracal predation on domestic animals (Chapter 2; Leighton et al. 2020), exposure to tick-borne pathogens in the study population points to possible pathogen spillover (Viljoen et al. 2020). When the costs outweigh the benefits, human-modified areas may become population sinks or ecological traps, where continued use of attractive, but harmful, environments often leads to local extinction (Battin 2004; Robertson et al. 2013). Mitigative conservation measures to prevent a potential trap include reduced use of pesticides and maintenance of cover, particularly around vineyards and at the urban edge, and traffic calming measures where roads bisect frequent crossing points. Further to reducing anthropogenic mortality of wildlife, the work of local

government and conservation agencies in maintaining and restoring connectivity between foraging habitats is essential for the continued ecological success of medium-sized carnivores like caracals, which persist despite extensive urbanisation of our cities.

CHAPTER 4

POISONED CHALICE: THE USE OF HUMAN LANDSCAPES BY CAPE TOWN'S CARACAL INCREASES THEIR EXPOSURE TO IMMUNOTOXIC PERSISTENT ORGANIC POLLUTANTS



ABSTRACT

Wildlife in and around cities bioaccumulate multiple harmful environmental pollutants associated with human activities, such as industrial chemicals and pesticides. Exposure severity can vary based on species behavioural traits and habitat use which can, in turn, be examined to elucidate exposure pathways. Carnivores play vital roles in ecosystem stability but are particularly vulnerable to bioaccumulation of pollutants. Understanding the sources of these contaminants can inform pollutant control, and carnivores, at the top of food webs, can therefore act as useful indicator species. Here I test for prevalence and level of exposure to commonly detected toxic organochlorine (OC) compounds, including DDT and PCBs, in a medium-sized felid, the caracal (*Caracal caracal*), across the peri-urban and agricultural landscapes of the city of Cape Town, South Africa. Concentrations in both blood (n = 69) and adipose (n = 25) tissue were estimated using gas chromatography, and were analysed along with detailed spatial, dietary, and demographic data to assess OC sources and exposure risk. The analysis revealed widespread exposure of Cape Town's caracal to organochlorines: 100% exposure to PCBs and 83% exposure to DDTs in blood, and 100% exposure to both compounds in adipose tissue. Caracals using transformed areas of the city, such as vineyards and areas with higher human population and electrical transformer density, as well as wetland areas, have higher organochlorine burdens. These landscapes are also strongly selected foraging areas, suggesting caracal are drawn into areas that, while serving as successful foraging areas, co-incidentally increase their risk of exposure to these pollutants. Additionally, I report possible physiological effects of exposure, including elevated white blood cell and platelet count, suggesting a degree of immunological response that may increase disease susceptibility. These sublethal effects may impact fitness, potentially leading to a population decline. Cape Town's urban fringes likely represent a toxic ecological trap for wildlife generally and require focused attention and action to ensure persistence of this adaptable carnivore.

INTRODUCTION

Wildlife in urban areas are challenged by multiple novel stressors, including noise and light pollution, human and machine disturbance, and increasingly, toxic environmental pollutants (French et al. 2018; Rodríguez-Estival and Mateo 2019; Sánchez et al. 2020). Human activities in urban and agricultural areas import large quantities of novel persistent organic pollutants (POPs; including industrial chemicals and pesticides), which may then spread directly into neighbouring natural systems, or indirectly through long-distance atmospheric transfer (Risebrough et al. 1976; Geisz et al. 2009; Borgå 2019), and remain in ecosystems for long periods (Smith et al. 2007). Once they enter ecosystems, POPs can exert a number of harmful effects on the physiology of wildlife species, including neurotoxicity, carcinogenesis, hormone

disruption (Barni et al. 2016; Nossen et al. 2016), behavioural changes (Iwaniuk et al. 2006; DeLeon et al. 2013), reproductive impairment (Vos et al. 2000; Da Cuña et al. 2011; Byer et al. 2015), altered immune function, and potentially increased disease susceptibility (Lie et al. 2005; Mori et al. 2006; Finkelstein et al. 2007; Vos 2007). Consequently, species in or adjacent to urban ecosystems exposed to an array of toxic compounds frequently present with a higher likelihood of infection and diversity of parasites than those in natural areas (Murray et al. 2019). This relationship between increased toxicant exposure and reduced health is likely to worsen through "chemical intensification", i.e., the increased production and use of synthetic, complex chemicals both locally and globally (United Nations Environmental Programme 2013; Diamond et al. 2015), and through global warming driving increased release of pollutants from soil and ice reservoirs (Burek et al. 2008; Geisz et al. 2009; Ma et al. 2016).

The release of POPs into the environment can either be through intentional use of pesticides (e.g., commercial preparations like aldrin, chlordane, dichloro-diphenyl-trichloroethane [DDT]), or unintentionally through human activities, such as waste burning, mining, and construction (e.g., polychlorinated biphenyls [PCBs]; see Table 4.1). Wildlife exposure to the pollutants released into their environments is most common through dietary pathways (Berny 2007; Smith et al. 2007) with bioaccumulation evident at higher trophic levels of ecological food webs (Gobas et al. 1993; Walters et al. 2016; van den Brink et al. 2016). Exposure severity is linked to specific ecological traits of species, particularly those associated with foraging strategy and diet, together with habitat use (Christensen et al. 2005; Smith et al. 2007; Andersen et al. 2015). For example, diet composition, higher trophic status and food handling behaviours can all influence dietary exposure (Smith et al. 2007). Because POPs have low water solubility the largest reservoirs are generally found in aquatic systems, particularly in wetland and ocean sediments (El-Shahawi et al. 2010), placing aquatic-dependent species and their predators at risk (Smith et al. 2007; Huang et al. 2018). Further, those species with higher use of human-transformed landscapes are more exposed (Garcia-Heras et al. 2018; Gómez-Ramírez et al. 2019; Buck et al. 2020). Identifying the most likely sources of POPS in the environment can inform our understanding of how species-specific behaviours and habitat use contribute to their risk of exposure. Furthermore, assessing temporal and spatial trends in pollutant exposure directly informs measures of the effectiveness of local pollutant control and mitigation measures by improving understanding of the sources of these harmful contaminants for both wildlife and humans (Colborn et al. 1993; Ross and Birnbaum 2003; Bench 2003; Malarvannan et al. 2020).

Under the holistic "Global One Health Paradigm" there is increasing need to recognise the interdependence of human and wildlife health, particularly in the face of recent and ongoing pandemics (Gebreyes et al. 2014; Bonilla-Aldana et al. 2020). Being at the apex of ecological food webs, carnivores are valuable indicators of ecosystem condition (Harley et al. 2016) and are disproportionately affected by pollutants through bioaccumulation and biomagnification (Corsolini et al. 2000; Harley et al. 2016; Rodríguez-Jorquera et al. 2017). Top carnivores can thus be used to evaluate the composition and extent of pollutants

present in both natural and transformed systems, providing insight into the risks and sources of exposure for humans and wildlife (Sergio et al. 2006; Jooste et al. 2013). Adverse health effects may also be correspondingly greater in top carnivores as a result of secondary and tertiary exposure; in turn, this may impact individual fitness and survival, and ultimately lead to population declines (Desforges et al. 2016). In both agricultural and urbanising landscapes, understanding the levels and consequences of pollutant exposure is important for the effective conservation of carnivores (Rodríguez-Jorquera et al. 2017; Rodríguez-Estival and Mateo 2019), where they are also frequently threatened by persecution and habitat loss (Laliberte and Ripple 2004; Soulsbury and White 2015).

Despite their persistence and toxicity, there are limited studies assessing the occurrence of POPs in terrestrial top predators (Rodríguez-Jorquera et al. 2017), particularly on the African continent (Murray et al. 2019; Rodríguez-Estival and Mateo 2019). In many African countries, the illegal use of chemicals is common and the regulations on the sale and use of pesticides are few and poorly observed (Osibanjo et al. 2002; Bouwman 2003; Mansour 2004; Ogada 2014). Moreover, pesticides are often incorrectly applied and stored, which has consequences for the effectiveness of pest control, as well as for contamination of the surrounding environment, livestock, wildlife and for human health (Sibanda et al. 2000; Pretty and Waibel 2005; Williamson et al. 2008). Even though the Stockholm Convention (2001) banned the use of POPs in South Africa (Bouwman 2004), the country remains among the largest importers of pesticides in sub-Saharan Africa (Osibanjo et al. 2002; Quinn et al. 2011), while legacy organochlorines (OCs; see Table 4.1) are still detected at some of the highest concentrations globally (e.g., DDT, dichloro-diphenyl-trichloroethane: Wells and Leonard 2006; hexachlorocyclohexanes, HCHs: Ogata et al. 2009). The potential for spillover of POPs adjacent to South Africa's cities is therefore likely to be high with serious consequences for humans, livestock, and biodiversity (Bouwman 2003). Contaminated urban areas may therefore present a "poisoned chalice" for resident carnivores, attracted by the abundant and available prey associated with human-transformed landscapes (Bateman and Fleming 2012; Fleming and Bateman 2018; Hansen et al. 2020), which in turn is exposed to toxic mixtures of pesticides (Serieys et al. 2015, 2019; López-Perea and Mateo 2019; López-Perea et al. 2019; Lettoof et al. 2020). Carnivores must respond to the potential food resources around these cities while avoiding possible health and mortality risks. However, these risks are often not detectable to the animals, resulting in an ecological trap (e.g., Lamb et al. 2017; Huang et al. 2018; Johnson et al. 2020). Such traps occur in fast-changing environments when species inadvertently select poor quality habitats, ultimately leading to local extinction (Remeš 2000; Lamb et al. 2017; Fleming and Bateman 2018).

Around the rapidly expanding city of Cape Town, South Africa, caracals (*Caracal caracal*) selectively forage at the urban edge (Chapter 3; Leighton et al. 2021) but may unwittingly experience pollutant spillover through exposed prey species (Serieys et al. 2019). Here, I use the caracal as an indicator species to explore if Cape Town's transformed areas act as an ecological trap for wildlife by providing valuable foraging opportunities but increasing the probability of exposure to pollutants. Using gas chromatography methods to

quantify pollutant composition along with a linear mixed model approach, I analyse landscape-level organochlorine (OC) pollutant exposure risk for caracals across a gradient of landscape transformation and informed by detailed dietary (Chapter 2; Leighton et al. 2020), demographic, and spatial analyses. Additionally, I explore how OC levels may affect individual physiology, including body condition and haematological and serum parameters of caracal in the study area. Identifying and assessing exposure to stressors such as pollutants is crucial for conservation and management of wildlife living in transformed landscapes, with consequences for both wildlife and human health (Colborn et al. 1993; Lettoof et al. 2021). I therefore discuss the conservation implications of my findings on organochlorine levels for wildlife using urban areas and provide recommendations for mitigative measures.

METHODS

STUDY SITE

I assessed organochlorine exposure in samples collected from free-ranging caracals, both collared individuals with known home ranges on the Cape Peninsula (hereafter "Peninsula"), and opportunistically collected mortalities (mainly roadkill) around the greater area of the city of Cape Town, South Africa (Fig. 4.1). Cape Town has a long history of urban settlement and development together with agricultural land-use and industry (Anderson and O'Farrell 2012), resulting in a mosaic landscape composed of industrial regions, residential suburbs, informal settlements, greenbelts, sports fields, commercial vineyards and pine plantations, and protected wildland areas dominated by indigenous fynbos vegetation. According to municipal estimates there are over 290 informal settlements in the Greater Cape Town area (11.4% of households; Housing Development Agency 2012; City of Cape Town Government 2020). Mason and Fraser (1998) characterise an informal settlement as "a dense proliferation of small, makeshift shelters built from diverse materials (such as plastic, tin sheeting, and wooden planks)" which is associated with "degradation of the local ecosystem (e.g., erosion and poor water quality and sanitation)". The city surrounds Table Mountain National Park (TMNP), a UNESCO World Heritage Site and Biodiversity Hotspot (Fig. 4.1).

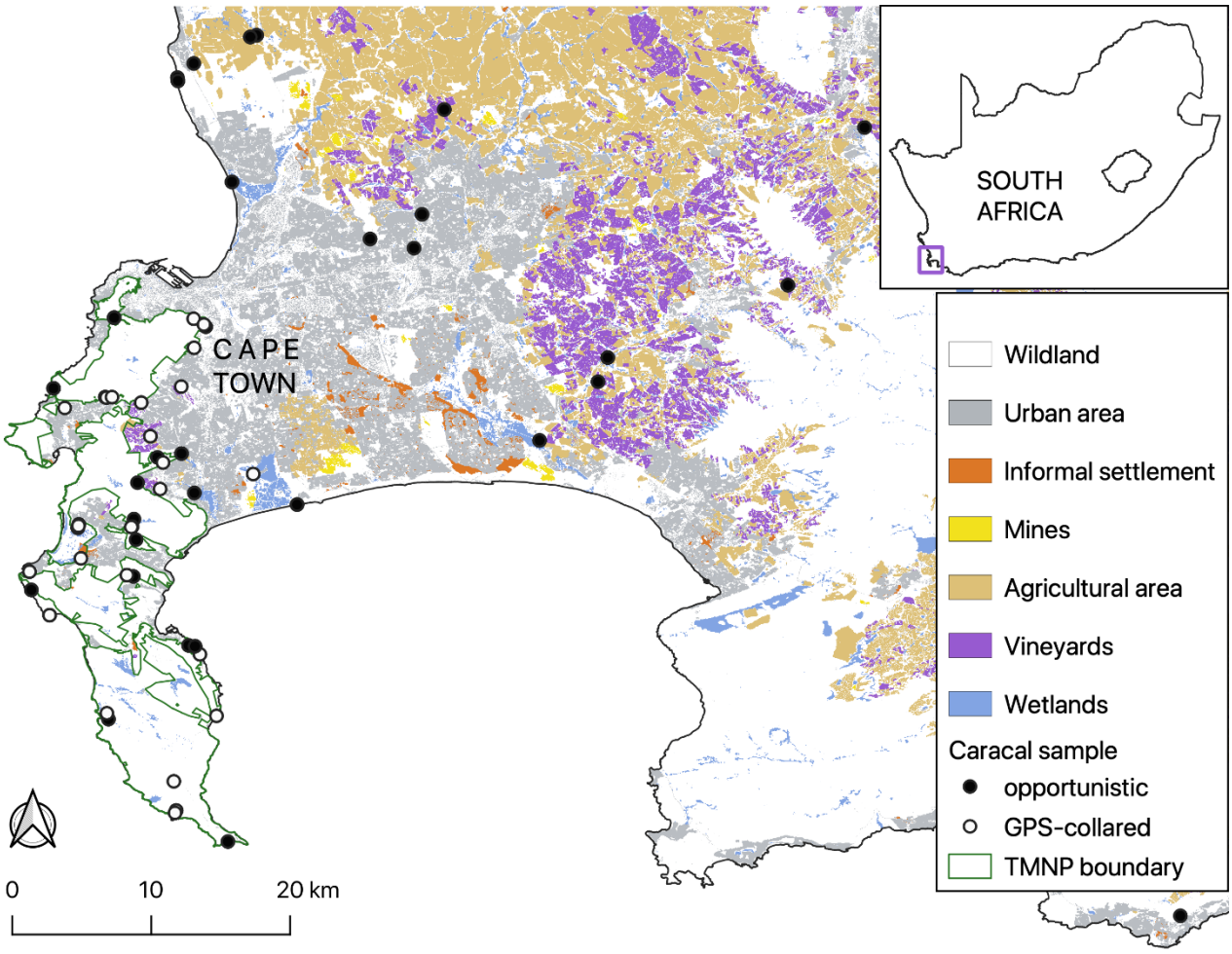


Fig. 4.1 Map showing locations of individual caracal sampled for pollutants in the Greater Cape Town area, South Africa. White circles are capture locations of caracal individuals that were trapped and collared with GPS tracking devices. Black circles are opportunistically sampled individuals with buffers calculated around collection location that were mostly killed in vehicle accidents. Coloured areas on the map correspond to different land uses. The green line denotes the Table Mountain National Park (TMNP) boundary.

Sampling

Standard cage-trapping techniques were used to capture and GPS-collar caracals between 2014 – 2016 to obtain movement and habitat use data (detailed capture and collaring methods described in Chapter 2). Additionally, caracal carcasses were opportunistically collected and necropsied throughout the study area. For each individual age class, sex, weight, and morphological measurements were recorded. Individuals were classified as subadults (< 2 years) or adults (≥ 2 years; see Chapter 2). Blood samples were collected at captures, recaptures and from necropsied individuals, and adipose samples were collected at necropsies. Samples were stored at -20°C in cryotubes (Greiner Bio-One Cryo.s™ Tubes). All sampling protocols followed ethical guidelines and permitting (see Chapter 1 for details).

ORGANOCHLORINE ANALYSIS

Organochlorine concentrations were determined in both caracal blood (1 g) and adipose tissue (0.5 g) following Mateo et al. (2012) using an *n*-hexane extraction, sulfuric acid clean-up and analysis by gas chromatography coupled to an electron capture detector (GC-ECD; Agilent Technologies 6890 N series; see Mateo et al. 2012 for specific details). Blanks and fortified samples were processed among samples to assure quality of analyses. Although POPs can be exchangeable between tissues, blood usually informs recent, short-term exposure while adipose can inform exposure over longer term due to accumulation and storage of OCs in this tissue type. PCBs and DDTs are highly environmentally stable and have half-lives of up to 15 years (Blaylock 2005; Ritter et al. 2011). Recovery of target OCs were > 80% and the limit of detection was 0.01 ng/g wet weight (w.w.). The concentrations (ng/mg) are expressed in w.w. and lipid weight (l.w.) to allow comparison with other studies. Here, I focus on results obtained for the compounds with an occurrence > 80% and proportionally higher concentrations in both sample types (DDTs and PCBs, especially PCBs #153 and #180; see Table 4.1) and use these data to explore their relationship to habitat use, diet, haematology, and plasma biochemistry of caracals. The results of other OCs are given in Appendix 4.1. Organochlorine analysis was carried out in the ecotoxicology laboratory at the Instituto de Investigación en Recursos Cinegéticos (IREC), Ciudad Real, Spain.

Table 4.1 Descriptions and potential sources of the main organochlorine compounds tested in caracal tissues in South Africa*.

Compound	Description	Sources	Health impacts
DDT	Dichloro-diphenyl-trichloroethane	Spraying for insect control in agricultural and malaria areas	Synthetic endocrine disrupter and carcinogen
***p,p'*-DDE**	para, para' -Dichloro-diphenyl-dichloroethylene (isomer of DDT)	Xenobiotic metabolite and environmental breakdown product of DDT found in humans and wildlife	Endocrine disrupter and carcinogen
PCB	Polychlorinated biphenyl; 209 possible congeners. More chlorinated PCBs are more lipophilic, less volatile and less water soluble. PCBs are typically used as mixtures of compounds and around 130 different individual PCBs are found in commercial PCB products	Found in dielectric and coolant fluids in electrical apparatus, in carbonless copy paper and in heat transfer fluids, plasticisers in paints and cements, pesticide extenders, reactive flame retardants and sealants for caulking, adhesives, wood floor finishes, de-dusting agents, waterproofing compounds, casting agent, ink pigments	Synthetic endocrine disrupters and neurotoxins, carcinogenic and teratogenic
PCB-153	Polychlorinated biphenyl with 153 chlorine substituents; #153 is a di-*ortho* substituted non-	As above	As above

Compound	Description	Sources	Health impacts
	coplanar congener commonly found in humans and wildlife		
PCB-180	Polychlorinated biphenyl with 180 chlorine substituents; #180 is a di-*ortho* substituted non-coplanar congener commonly found in humans and wildlife	As above	As above

*Information from: United Nations Environment Programme et al. 1989; Kelce et al. 1995; United Nations Environmental Programme 1999; World Health Organization 2000; Blaylock 2005; Rossberg et al. 2006; Rudel et al. 2008.

i. Blood sample extraction

A measure of 1 g of blood was added to 7 g sodium sulphate and homogenised with a mortar and pestle. The homogenised sample was then transferred to a 30 mL glass vial with a Teflon-lined cap and 10 µL isooctane (keeper) and 10 µL internal standard (PCB #209, deuterated PBDE #77, #181, #209) was added, as well as 7 mL *n*-hexane. The vial was vortexed for 1 minute, exposed to ultrasound for 10 minutes and centrifuged for 5 minutes at 2500 rpm. The resultant hexane solution was pipetted into a 15mL glass tube and dried under a stream of N_2 gas. This was repeated three times. The first two times, the solution was not allowed to dry past 1 mL and the final time the tube was dried completely, and the fat content estimated by gravimetry. The samples were then resuspended in 3 mL hexane. The clean-up step was performed by adding 1 mL of concentrated sulphuric acid, then the tubes were softly shaken horizontally for 10 minutes and centrifuged at 2500 rpm for 5 minutes. This procedure was repeated twice with 1 mL of sulphuric acid, or until the hexane was clear. This solution was then dried under a stream of N_2 gas and resuspended in 100 µL *n*-hexane for GC-ECD analysis.

ii. Adipose sample extraction

For adipose tissue extraction, 0.5 g of adipose was spiked with 10 µL of IS. Pressurised liquid extraction (PLE) was performed with 10 mL *n*-hexane. For the clean-up, 20 mL of hexane and 3 mL of sulphuric acid was added, and the solution was shaken horizontally for 5 minutes and centrifuged at 2500 rpm for 5 minutes. This was repeated three times (with 3 mL sulphuric acid), or until the hexane solution was clear. In the first clean up, the sulphuric acid down phase was pipetted off, while in the second clean up the hexane solution was pipetted off into a new tube. This solution was then dried under a stream of N_2 gas in a conical tube and resuspended in 500 µL *n*-hexane for instrumental analysis (GC-ECD). The adipose weight was calculated as the adipose sample weight subtracted by the weight of the connective tissue remaining after extraction.

MEASURING CARACAL LANDSCAPE USE

Differences in caracal habitat use may affect individual exposure to organochlorines due to varying levels of contamination in local prey. PCB levels are expected to be higher closer to urban development due to higher use of electrical equipment (for electricity generation and mining) and certain household products, such as plasticised paints and flame retardants (Fiedler 2002; Bench 2003; Gioia et al. 2014; Table 4.1). In electrical equipment, such as transformers and switchgears, PCBs are used as insulating fluids (Table 4.1). DDT levels (including metabolites) in tissues are expected to be higher where there is more wetland habitat (due to historic mosquito control in the country and because they are low points to which most water drains) and agricultural land use (due to historic and ongoing crop pest control via pesticide application) in the home range of individuals (Wells and Leonard 2006; Pisa and Bouwman 2020).

The 2018 Department of Environmental Affairs (DEA) landcover raster was used to calculate the relative proportions of urban, agricultural, vineyards, wetland, informal settlement, mining, and wildland area, together with the average electrical transformer density and human population density within home ranges of each collared caracal (n = 25; see Table 4.2 for landscape predictor variable information). I calculated 95% LoCoH-*a* (adaptive) home ranges for animals for which I had a minimum of 30 days of three-hour fix interval movement data (Getz et al. 2007) implemented in *t-locoh* (Lyons et al. 2013; see Chapter 3 for details). For opportunistically sampled caracals (n = 31), I calculated these spatial variables within a circular buffer around the GPS location where the animal was found. Buffers were sized to obtain the mean caracal home range size for females (mean home range = 16.2 km^2), adult males (69.9 km^2) and subadult males (38.3 km^2; Serieys et al. *in review*). For recaptured individuals and mortalities, I had data on ranges after sampling, but for captured individuals, I assumed similar space use pre- and post-sampling.

I created binary rasters of each land-use type (Table 4.2) and density rasters (for human population and electrical transformers) and determined the mean values within each home range polygon or buffer circle. Location data for all electrical transformers and substations in the study area (either maintained by the Electricity Supply Commission of South Africa [Eskom Holdings SOC Ltd] or the City of Cape Town) were used to calculate the electrical transformer density raster. Data were provided under agreements with both Eskom and the City of Cape Town.

Table 4.2 Data sources and descriptions of the demographic and spatial predictor variables considered for models of organochlorine exposure in caracal in the Greater Cape Town area, South Africa. The binary rasters of each land-use type and the density rasters (for human population and electrical transformers) were used to determine the mean values within each home range polygon or buffer circle.

Variable	Type	Range	Source	Description
URBAN	Binary	0 – 1	South African Department of Environmental Affairs (DEA) Land-cover 2018 raster (egis.environment.gov.za/gis_data_downloads)	20 m resolution. 73 categories simplified to 2 (1 = urban, 0 = non-urban)
AGRICULTURAL	Binary	0 – 1	South African Department of Environmental Affairs (DEA) Land-cover 2018 raster (egis.environment.gov.za/gis_data_downloads)	20 m resolution. 73 categories simplified to 2 (1 = agricultural, 0 = non-agricultural)
VINEYARDS	Binary	0 – 1	South African Department of Environmental Affairs (DEA) Land-cover 2018 raster (egis.environment.gov.za/gis_data_downloads)	20 m resolution. 73 categories simplified to 2 (1 = vineyard, 0 = non-vineyard)
WETLANDS	Binary	0 – 1	South African Department of Environmental Affairs (DEA) Land-cover 2018 raster (egis.environment.gov.za/gis_data_downloads)	20 m resolution. 73 categories simplified to 2 (1 = wetland, 0 = non-wetland)
INFORMAL SETTLEMENTS	Binary	0 – 1	South African Department of Environmental Affairs (DEA) Land-cover 2018 raster (egis.environment.gov.za/gis_data_downloads)	20 m resolution. 73 categories simplified to 2 (1 = informal settlement, 0 = non-informal settlement)
ELECTRICAL TRANSFORMER DENSITY	Continuous	0 – 65	In the study area, the electricity generation authority is dependent on the suburb and is either managed by the national provider, Eskom, or the City of Cape Town. I joined GPS locations of all electrical transformers and substations managed by both ESKOM and City of Cape Town to create a density raster. Data provided under agreements from both Eskom and the City of Cape Town	100 m resolution
HUMAN POPULATION DENSITY	Continuous	0.01 – 77	A dataset generated by machine learning to identify buildings overlaid with census data created in May 2019. Facebook Connectivity Lab and Center for International Earth Science Information Network - CIESIN - Columbia University. 2016. High Resolution Settlement Layer (HRSL). Source imagery for HRSL © 2016 DigitalGlobe. https://data.humdata.org/dataset/highresolutionpopulationdensitymaps-zaf	30 m resolution
DEMOGRAPHIC	Categorical	1 – 3	This study. Due to low sample size, adult and subadult females were considered together as a single category	1 = adult male, 2 = subadult male, 3 = female
HOME RANGE	Categorical	0 – 1	This study	1 = collared individuals with an estimated home range, 0 = opportunistic individuals with a calculated circular buffer around collection point

DIET PROPORTION ESTIMATES

Dietary pathways are major potential sources of pollutants, where exposure can vary depending on prey choice (Christensen et al. 2005; Smith et al. 2007). Increased consumption of higher trophic level prey (i.e., other carnivores), synanthropic prey (i.e., human-associated) and exotic prey (e.g., introduced species, pets and livestock) is expected to be associated with higher organochlorine exposure (Smith et al. 2007). I therefore assessed the influence of foraging behaviour and diet on caracal OC exposure. The diet of collared caracal individuals with home ranges was previously described by integrating scat and GPS cluster analysis to obtain comprehensive estimates (Chapter 2; Leighton et al. 2020). I calculated diet proportions based on both biomass and frequency of occurrence (FO) per caracal individual. First, I investigated how OC exposure (with concentration of each OC as response variable) was influenced by dietary patterns using broad taxonomic groups (proportion bird, mammal, reptile, insect; Appendix 3.5) as predictor variables. Next, I looked in more detail at prey functional groups (carnivore, insectivore, granivore, herbivore, omnivore, and marine feeder). I then investigated dietary patterns for prey species foraging in different habitat types (i.e., in terrestrial, wetland, arboreal and marine environments). Finally, I investigated OC exposure between different prey groups based on level of human association, viz., wild, synanthropic and exotic.

HAEMATOLOGICAL, SERUM CHEMISTRY, AND BODY CONDITION PARAMETERS

Using blood pathology data for the GPS-collared caracals I explored possible associated physiological or stress responses to OC exposure. Caracals with higher OC exposure may present with lower body condition and increased chance of being immunocompromised or stressed (Davis et al. 2008; Murray et al. 2019). Complete blood-work was available for all collared individuals, including cell counts (total white and red blood cell count, neutrophil, lymphocyte, eosinophil, monocyte, basophil and platelet count, haemoglobin, mean corpuscular volume, mean corpuscular haemoglobin concentration and red cell distribution width) and serum biochemistry (total serum protein, albumin, globulins, albumin:globulins ratio, alanine transaminase (ALT), alkaline phosphatase (ALP), total bilirubin, urea, creatinine, phosphate, Cl^-, Na^+, K^+ concentration and Na:K ratio). Comprehensive blood-work analysis was carried out by Vet Diagnostix (veterinary pathology services, Cape Town, South Africa) or Penzance Veterinary Clinic (Cape Town, South Africa). White blood cells (e.g., neutrophils and lymphocytes) give insight into immune responses to stress, injury or infection (Davis et al. 2008). Neutrophils form part of the response of the innate immune system while lymphocytes take part in adaptive responses (e.g., immunoglobulin production). As a composite measure of stress I calculated the neutrophil to lymphocyte ratio (N:L ratio), which can be influenced by the disease and infection status of an individual (Davis et al. 2008). Body condition index (BCI) was also calculated based on Ordinary Least Squares (OLS; Labocha et al. 2014), as well as the Scaled Mass Index (SMI; Peig and Green 2009) per individual. The SMI is an alternative method to OLS residuals which accounts for allometric scaling, standardising body size

when calculating the condition index (Peig and Green 2009). These indices were calculated separately for ages and sexes.

STATISTICAL ANALYSES

To assess how caracal landscape use (Table 4.2) influences exposure to organochlorines (OCs) in blood and adipose tissue I applied linear mixed models (LMMs) using the "lmer*"* function in the *lme4* package (Bates et al. 2012) in R (R Core Team 2020). I explored the relationship between demographic (age and sex) and spatial variables with concentration of ΣDDT (including o,p'-DDE, p,p'-DDE, o,p'-DDD, p,p'-DDD, o,p'-DDT and p,p'-DDT), PCB-153, PCB-180 and ΣPCB (including PCB congeners #28, 52, 101, 153, 138 and 180), as the response variable in separate models for both wet and lipid weight. OC concentrations were not normally distributed (Shapiro-Wilk's $P < 0.001$) and hence were log-transformed. To incorporate all caracal samples (those with known home ranges and those opportunistically sampled) I included the spatial variable extraction method (home range area for collared individuals and buffer area for opportunistic mortalities) as a binary random effect (home range = 1, buffer = 0). Next, I ran linear models (using *lm*) to assess sources of OCs in diet using blood samples and detailed individual diet data (Chapter 2; Leighton et al. 2020); data were analysed in terms of both wet and lipid weight to facilitate comparison with other studies. I ran separate models for each OC contaminant for broad taxonomic prey groups, functional groups, foraging habitats, and prey types. Finally, I tested for physiological effects of OCs by running linear models of OC concentration with blood cell counts, serum biochemistry parameters, and body condition indices.

I assessed multicollinearity in my covariates and retained only independent variables (VIF < 5; James et al. 2013). All covariates were scaled and centred. I selected the top model using AICc (Burnham and Anderson 2002) by fitting models with all covariate permutations (using dredge in the *MuMin* package; Bartoń 2020). Exposure risk surfaces based on the best models for ΣDDT and ΣPCB were created by predicting exposure probability over rasters of used covariates with the "predict" function in R and discretising to five equal area levels before plotting (Morris et al. 2016) in QGIS (version 3.2.1-Bonn; QGIS Development Team 2020). All statistical analyses were conducted using R version 4.0.2 (2020-06-22) using preloaded packages.

RESULTS

EXPOSURE TO ORGANOCHLORINES IN THE STUDY AREA

A total of 69 blood samples and 25 fat samples (representing 56 individual caracals) were collected across the study area (Table 4.3). Of the blood samples, 36 were from GPS-collared individuals with known home ranges (23 captures, six recaptures and seven mortalities representing 24 unique individuals) while 33

were opportunistically collected and buffers calculated. For adipose tissue samples, six were collected from deceased collared individuals with known home ranges and 19 were from opportunistically sampled individuals.

Table 4.3 Caracal samples tested for organochlorine (OC) contaminants in the Greater Cape Town area, South Africa (n = 56 unique individuals).

Tissue	Sampling	Demographic	n
adipose (n = 25)	GPS-collared	female	1
		subadult male	3
		adult male	2
	opportunistic	female	7
		subadult male	7
		adult male	5
blood (n = 69)	GPS-collared	female	11
		subadult male	11
		adult male	14
	opportunistic	female	13
		subadult male	13
		adult male	7

Using GC-ECD I obtained and confirmed concentrations for 26 organochlorine compounds from the blood and adipose samples (concentrations summarised in Appendix 4.1). Five blood samples had no lipid weight and so concentrations expressed in lipid weight could not be calculated. Exposure to OCs was high; I detected PCBs in 100% of blood samples, while DDT exposure was recorded in 83% of blood samples. Adipose samples revealed 100% exposure to both PCBs and DDT, with higher concentrations than in blood. The dominant PCB congeners identified in samples were PCB-180 and PCB-153, although PCB-138 and PCB-101 were also detected (Appendix 4.1 and 4.2). Concentrations of the metabolite p,p'-DDE were on average higher than p,p'-DDT (Appendix 4.1 and 4.2).

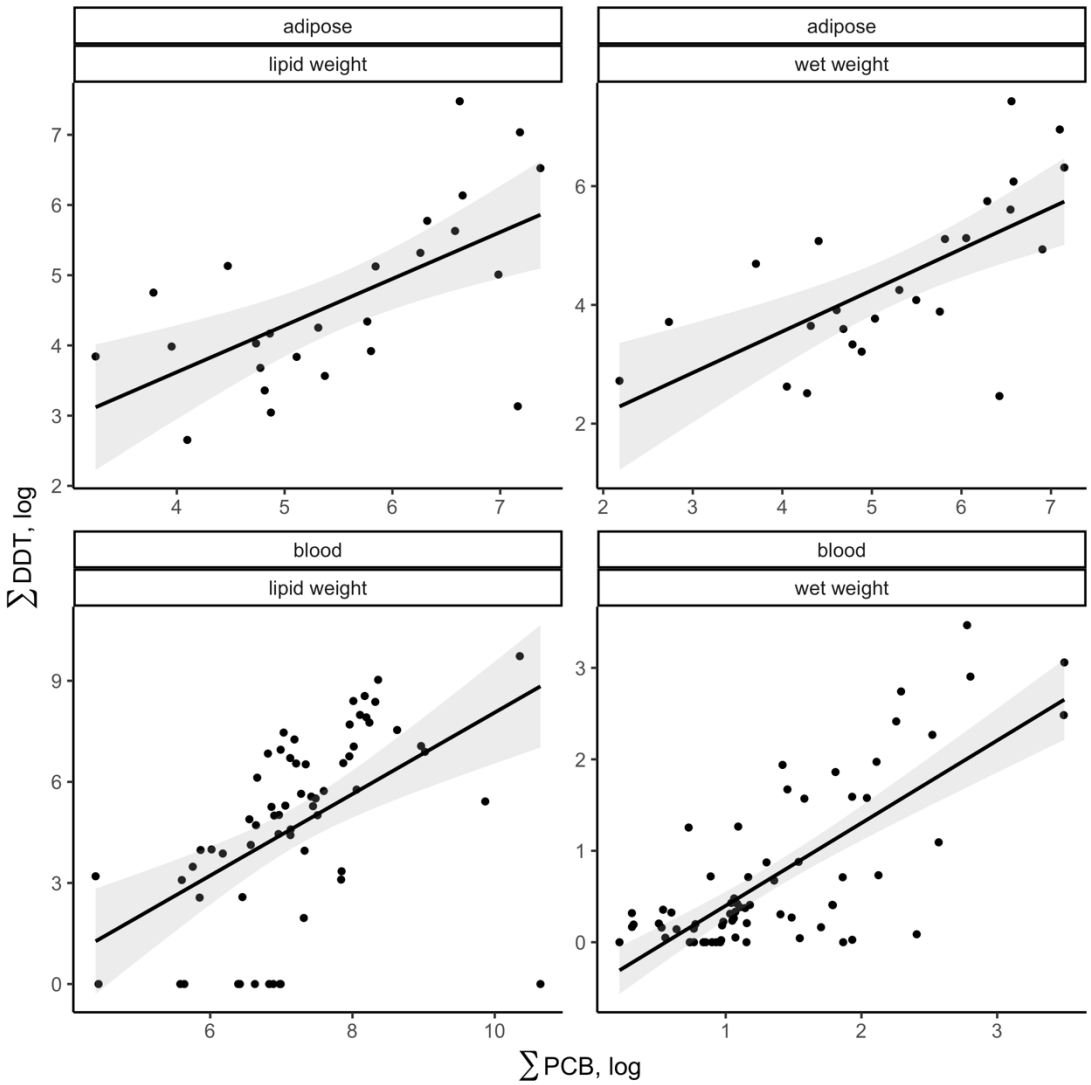


Fig. 4.2 Relationship between logged concentration of ΣPCB and ΣDDT in adipose and whole blood of caracals from the Greater Cape Town area, South Africa. All relationships were highly significant ($p < 0.001$).

As expected for bioaccumulated non-polar contaminants, organochlorine concentrations were correlated between residues in both blood ($F_{1,62} = 21.94$, $P < 0.001$ l.w. and $F_{1,67} = 84.33$, $P < 0.001$ w.w.) and adipose ($F_{1,23} = 13.76$, $P < 0.001$ l.w. and $F_{1,23} = 18.19$, $P < 0.001$ w.w.; Fig. 4.2). Adipose concentrations were, on average, higher than blood concentrations due to accumulation in tissues with higher lipid content ($P < 0.05$ in both blood and adipose tissue; see Appendix 4.1), except for lipid weight of ΣDDT, which was not significantly higher in adipose ($F_{1,87} = 0.03$, $P = 0.86$). In general, individuals that were opportunistically sampled did not have significantly higher levels of exposure to logged ΣDDT and ΣPCB than collared individuals ($P > 0.05$ in both blood and adipose tissue), except in the case of wet weight of adipose ΣDDT, where collared individuals had lower concentrations ($F_{1,23} = 4.54$, $P = 0.04$; mean collared = 107 ± 218 ng/g, mean opportunistic = 257 ± 420 ng/g).

There were no significant differences between demographic groups for logged ΣDDT concentrations in adipose ($F_{1,22}$ = 1.33, *P* = 0.28 l.w. and $F_{1,22}$ = 0.83, *P* = 0.45 w.w) or blood concentrations in lipid weight ($F_{2,61}$ = 0.64, *P* = 0.53). However, blood concentrations in wet weight were marginally higher in subadult males ($F_{2,66}$ = 2.76, *P* = 0.07). For adipose ΣPCB females and subadult males were higher than adult males ($F_{1,22}$ = 4.78, *P* = 0.02) when comparing lipid weight and marginally significant for wet weight ($F_{1,22}$ = 2.72, *P* = 0.09). ΣPCB levels were not significantly different for blood concentrations in lipid weight ($F_{2,61}$ = 0.64, *P* = 0.53) but blood concentrations in wet weight were significantly different, where subadult males were highest ($F_{2,66}$ = 3.57, *P* = 0.03).

Subadult males had a higher proportion of urban area in their home ranges ($F_{2,29}$ = 7.42, *P* < 0.01) and buffer zones ($F_{2,29}$ = 2.88, *P* = 0.07) a higher density of transformers in both their home ranges ($F_{2,29}$ = 4, *P* < 0.05) and buffer zones ($F_{2,29}$ = 4.25, *P* < 0.05) than adult males and females. Subadult males also consumed a higher proportion of "human-subsidised" (i.e., both exotic and synanthropic) prey biomass (65.0%) than adult males (38.1%) and females (44.7%).

LANDSCAPE LEVEL SOURCES OF ORGANOCHLORINE EXPOSURE

Caracal home ranges and buffer areas mainly encompassed wildland areas (mean = 76.93% ± 19.62% SD), but individuals used several additional land-use types in the study area, highest of which were urban (overall mean = 16.21% ± 15.93 SD; Table 4.4) and agricultural (mean = 8.88% ± 18.25 SD; Table 4.4).

Table 4.4 The mean ± SD percentage of different land uses, human population density (30 m^2) and electrical transformer density (100 m^2) for GPS-collared (i.e., within the home ranges) and opportunistically sampled (i.e., within buffer areas) caracals in the Greater Cape Town area of the Western Cape, South Africa.

Tissue	Sampling	Agricultural	Informal settle-ment	Mines	Wildland	Urban	Vineyards	Wetlands	Population density	Transformer density
Adipose	GPS-collared	5.74 ± 8.97	0.51 ± 1.11	0.00 ± 0.00	84.15 ± 12.66	11.34 ± 8.55	4.54 ± 7.27	3.04 ± 3.69	3.28 ± 1.72	0.01 ± 0.01
	Opportunistic	16.85 ± 24.25	0.64 ± 1.25	0.44 ± 1.32	66.76 ± 16.99	21.12 ± 16.65	3.91 ± 8.90	5.01 ± 4.86	3.57 ± 2.52	0.05 ± 0.05
Blood	GPS-collared	3.27 ± 6.14	0.72 ± 1.17	0.40 ± 1.89	85.95 ± 11.01	11.41 ± 8.20	2.30 ± 4.77	5.15 ± 6.44	4.10 ± 2.84	0.02 ± 0.01
	Opportunistic	15.00 ± 24.34	0.40 ± 0.99	0.32 ± 1.04	67.09 ± 22.22	21.44 ± 20.28	4.18 ± 9.30	3.66 ± 4.10	4.12 ± 2.98	0.05 ± 0.06

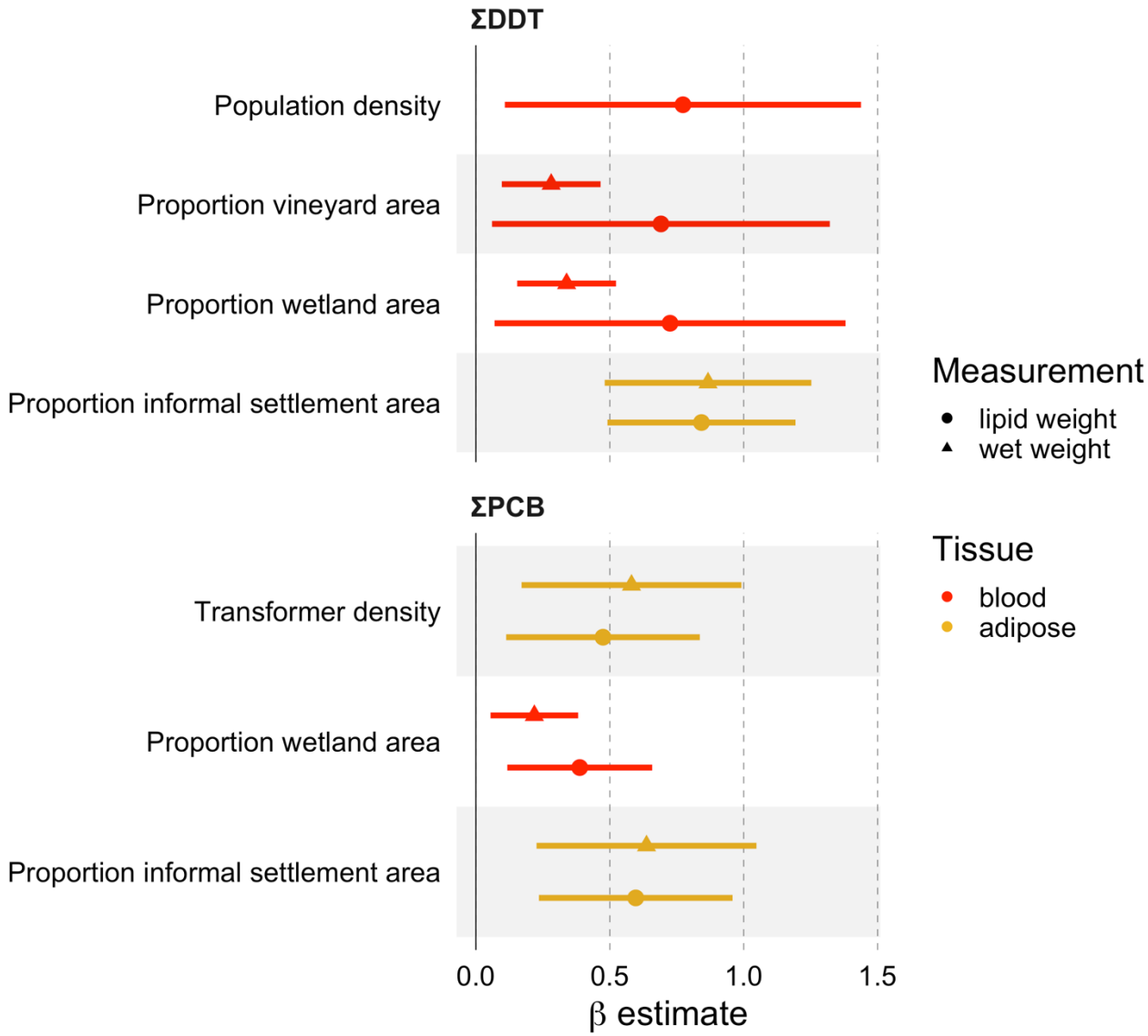


Fig. 4.3 Parameter estimates and 95% confidence intervals for spatial variable LMMs of caracal blood (red) and adipose (orange) for concentrations of organochlorines in terms of wet (circle) and lipid (triangle) weight. Estimates are shown for those parameters included in the top models (as determined by AICc) including different land uses, human population density and electrical transformer density in the Greater Cape Town area.

For DDT exposure measured in whole blood, those individuals using more wetland (β = 0.34 ± 0.09, $P < 0.01$) and vineyard area (β = 0.28 ± 0.09, $P < 0.01$) were more likely to be exposed (Fig. 4.3; Appendix 4.3), despite these landscape features being a small percentage of home ranges and buffer areas used (mean wetlands = 4.44% ± 5.46% SD; mean vineyards = 3.2% ± 7.3% SD; Table 4.4). Higher human population density was also a positive spatial predictor of DDT exposure in blood (β = 0.77 ± 0.34, $P < 0.01$; mean = 4.09 ± 2.93 SD people/30 m^2; Fig. 4.3 and Fig. 4.4A). For exposure in adipose tissue, the percentage informal settlement cover in home ranges and buffer areas was the strongest spatial predictor (ΣDDT: β = 0.87 ± 0.20, $P < 0.01$; ΣPCB: β = 0.64 ± 0.21, $P < 0.01$; Fig. 4.3), despite comprising a very small percentage of the area used by individuals (mean = 0.61% ± 1.09 SD; Table 4.4).

Use of wetland areas was a strong predictor of increased PCB burden (especially PCB-180; β = 0.38 ± 0.15, $P < 0.05$) in blood measures of exposure (Appendix 4.3). Again, in adipose, I found the proportion of informal settlement area was positively associated with levels of PCBs (especially PCB-153, β = 0.57 ± 0.20, $P < 0.01$). Further, those individuals that were exposed to higher density of electrical transformers (mean = 4.16 ± 4.68 SD transformers/km^2) had higher concentrations of PCBs in adipose (β = 0.58 ± 0.21, $P < 0.01$; Fig. 4.3 and Fig. 4.4B), particularly congener PCB-153 (β = 0.69 ± 0.20, $P < 0.01$; Appendix 4.4). However, I also found that those individuals living in areas with a higher human population density had higher levels of PCB-153 in blood (β = 0.49 ± 0.24, $P < 0.05$; Appendix 4.3), and those individuals living in more urbanised areas had higher levels of PCB-180 in adipose (β = 0.60 ± 0.21, $P < 0.01$, Appendix 4.4).

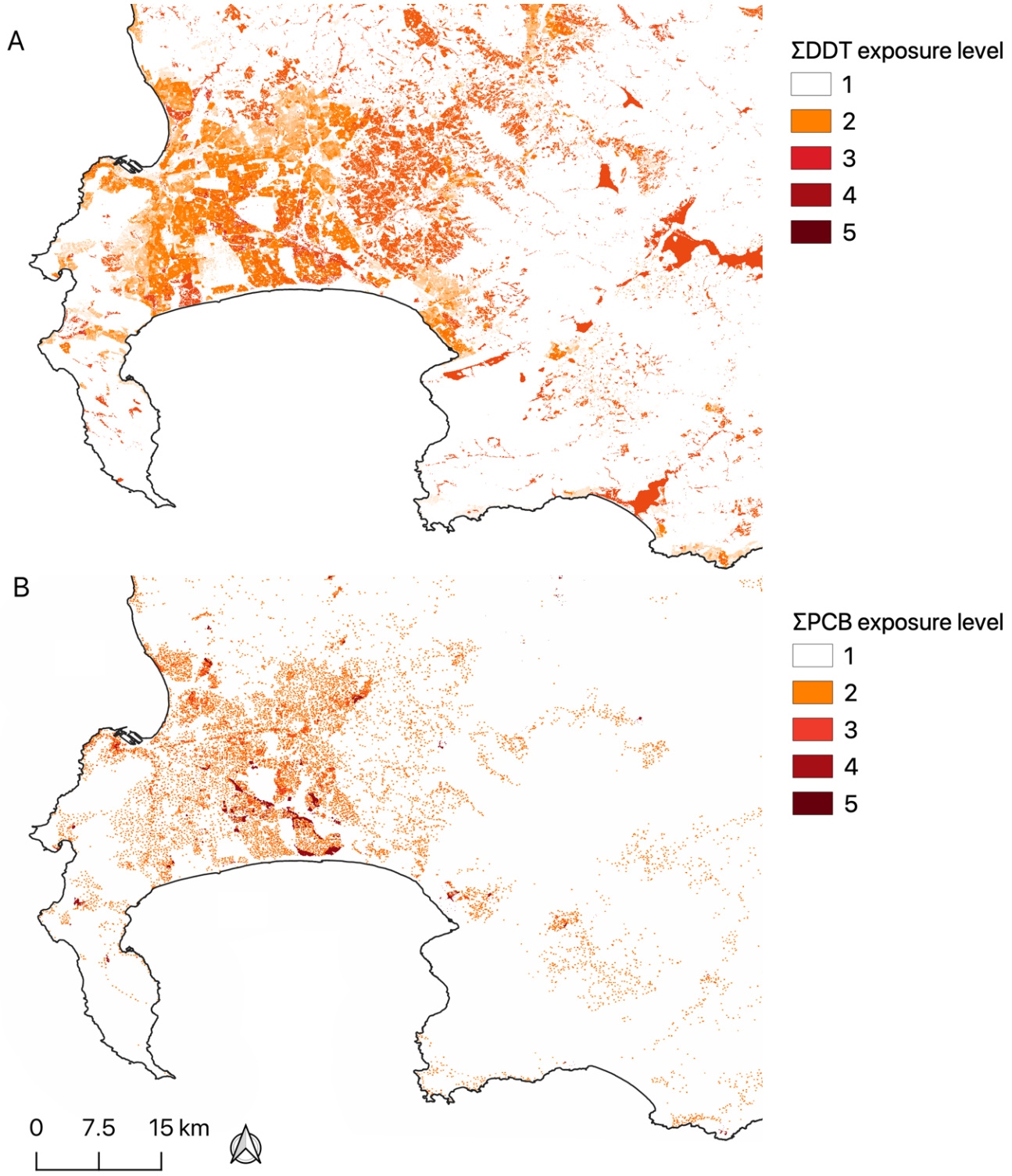


Fig. 4.4 Organochlorine exposure risk maps for the Greater Cape Town area showing probability of exposure categorised into five risk levels based on spatial variable LMMs which contained continuous variables: (**A**) ΣDDT (based on the top blood l.w. model which included wetlands, vineyards, and human population density) and (**B**) ΣPCB (based on the top adipose l.w. model which included informal settlements and electrical transformer density).

ORGANOCHLORINE EXPOSURE PATHWAYS THROUGH DIET

Using whole blood samples and detailed individual diet information (Chapter 2) I also explored how dietary patterns (measured across different prey groupings; Appendix 4.5) influence organochlorine exposure in terms of wet (n = 34) and lipid weight (n = 30). I only had sufficient dietary information to explore these patterns in blood.

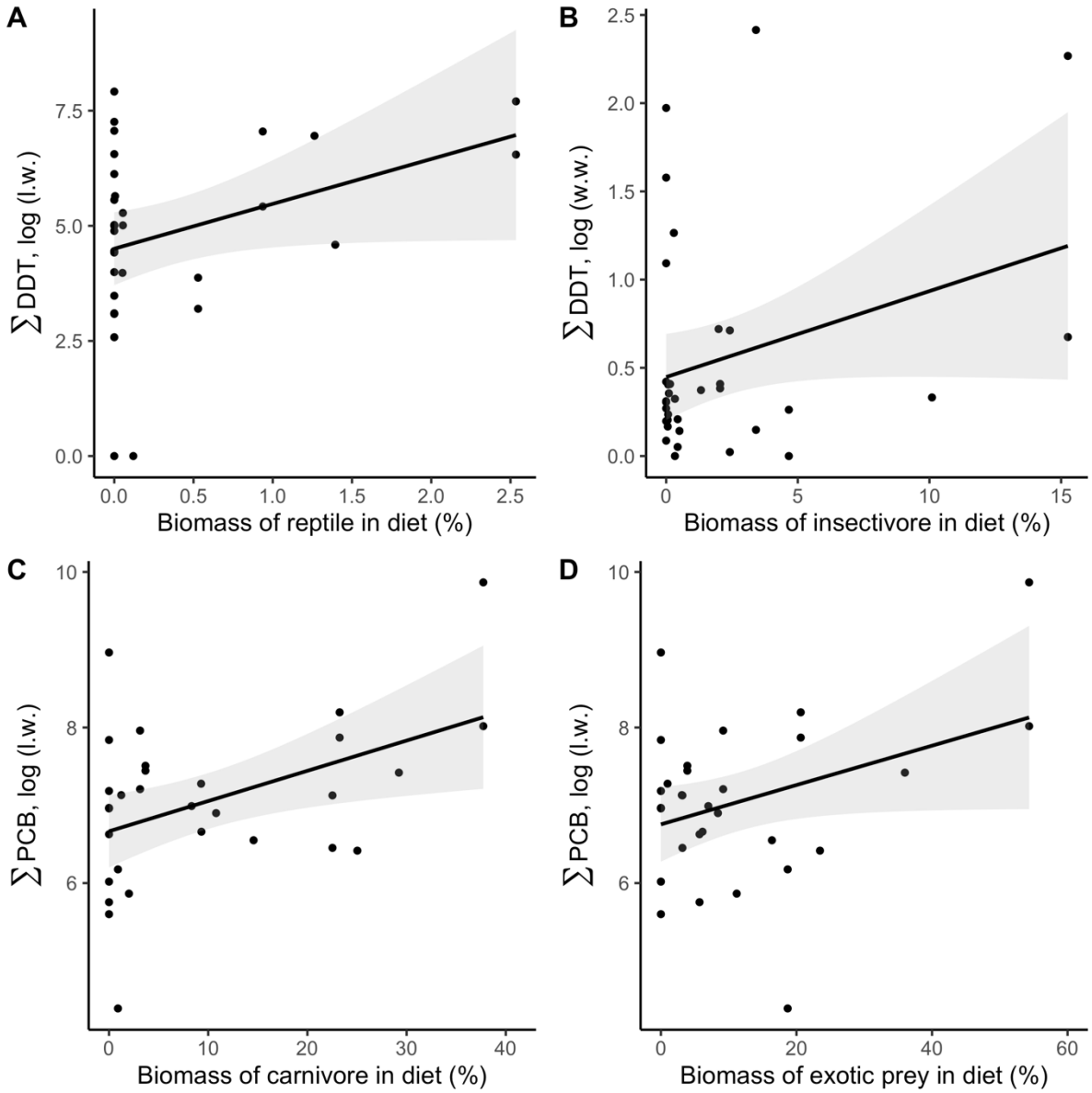


Fig. 4.5 Relationship between blood organochlorine concentrations (log-transformed) and percentage diet (biomass) of (**A**) reptile, (**B**) insectivore, (**C**) carnivore and (**D**) exotic prey for caracals around Cape Town, South Africa.

i. Broad taxonomic groups

An increase in proportion of reptile in diet increased caracal blood exposure to ΣDDT (β = 0.36 ± 0.10, $P < 0.01$ biomass: Appendix 4.6, and β = 0.34 ± 0.10 $P < 0.01$ FO: Appendix 4.7; Fig 4.5A), despite reptiles forming a very small component of the diet of the collared individuals (only 0.45% of biomass consumed,

2.87% frequency of occurrence [FO] in diet; Appendix 4.5). Reptile species included mole snakes (*Pseudaspis cana)*, puff adder (*Bitis arietans*) and black girdled lizard (*Cordylus niger*). There was also a strong negative association with ΣDDT concentration and proportion of insects consumed (β = -0.86 ± 0.31, $P < 0.05$ biomass; β = -0.72 ± 0.36, $P < 0.1$ FO; Appendix 4.6 and 4.7), which formed an even smaller proportion of diet (0.08% biomass, 0.96% FO; Appendix 4.5).

An increase in avian prey in the diet (46.20% biomass, 51.4% FO; Appendix 4.5) was also positively associated with exposure to PCB-153 (β = 0.48 ± 0.23, $P < 0.05$) and PCB-180 (β = 0.12 ± 0.07, $P < 0.1$, Appendix 4.6 and 4.7). The most common birds were Guinea fowl (*Numida meleagris*), Egyptian geese (*Alopochen aegyptiaca*), and Cape cormorants (*Phalacrocorax capensis*).

ii. Functional prey groups

Examining prey functional group allowed for a more detailed view of potential exposure pathways through prey. Individuals consuming more insectivorous (i.e., insect-consuming; β=0.19 ± 0.11, $P < 0.1$, Fig. 4.5B) and carnivorous species had higher DDT burdens (β = 0.72 ± 0.35, $P < 0.05$, Fig. 4.5C; Appendix 4.8 and 4.9), although these functional groups formed very little of caracal diet (insectivore: 0.81% biomass consumed, 5.06% FO and carnivore: 9.63% biomass, 8.21% FO; Appendix 4.5). The most common insectivores consumed by caracals were shrews (*Crocidura cyanea* and *Crocidura flavenscens*) and golden moles (*Chrysochloris asiatica*), and the most common carnivores were domestic cats (*Felis catus*), Cape grey mongooses (*Galerella pulverulenta*), large spotted genets (*Genetta tigrina*), and mole snakes. Similarly, a strong positive association exists between PCB levels and the proportion of carnivores in the diet (β = 0.47 ± 0.18, $P < 0.05$, Fig. 4.6). Additionally, there was a strong negative relationship between herbivore consumption (51.6% biomass, 30.20% FO; Appendix 4.5) and PCBs in blood, particularly for PCB-153 and -180 (Fig. 4.6). Although not statistically significant ($P > 0.1$), there was some evidence of marine pathways of exposure, as PCB-180 was associated with frequency of occurrence of marine-feeding prey (β = 0.11 ± 0.07, Fig. 4.6), mainly Cape cormorant (*Phalacrocorax capensis*).

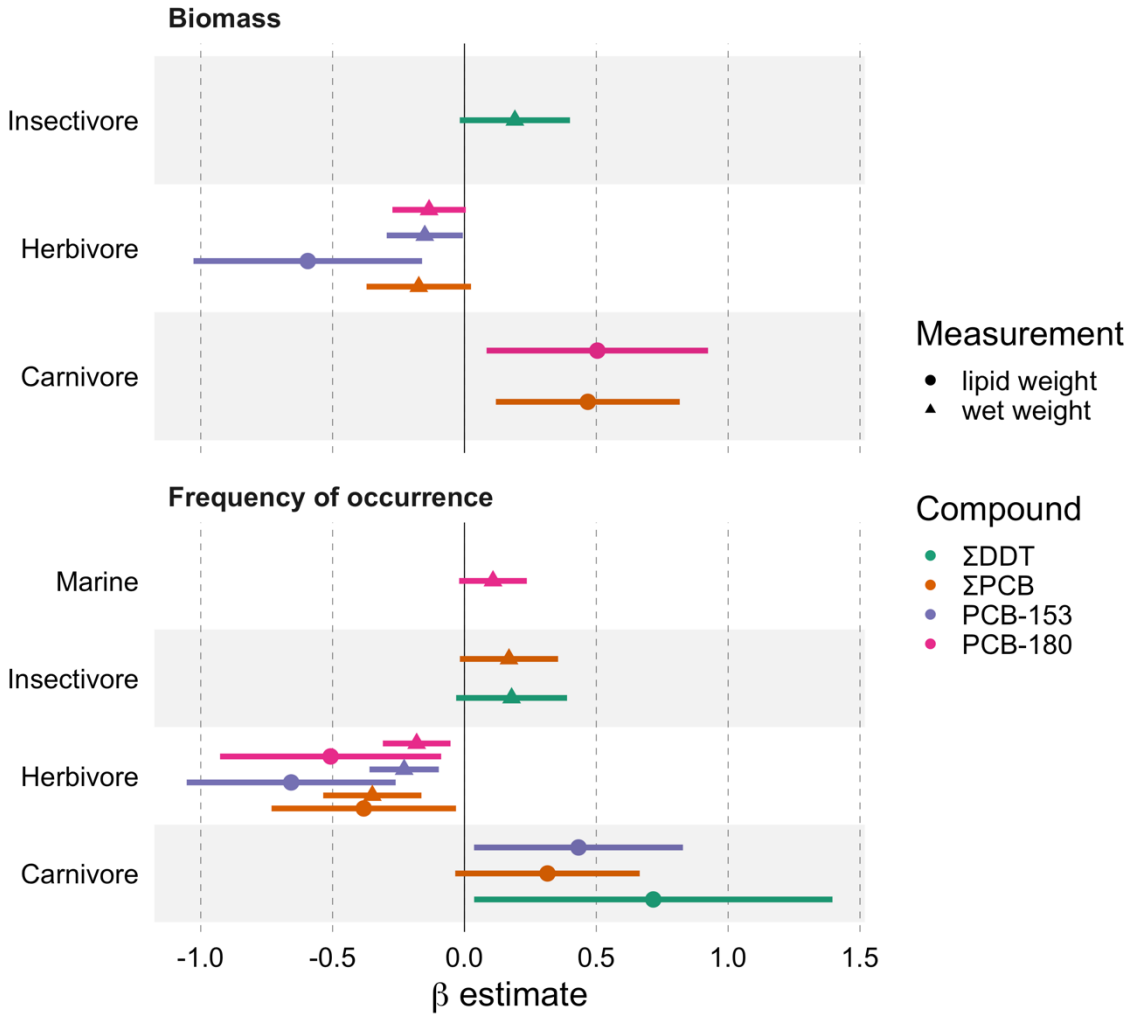


Fig. 4.6 Parameter estimates and 95% confidence intervals for linear models of diet proportion (prey functional groups) and concentrations of organochlorines in caracal blood in terms of wet (circle) and lipid (triangle) weight. Estimates are shown for those parameters included in the top models (as determined by AICc).

iii. Prey foraging habitat

Caracals were more likely to be exposed to OCs when feeding on wetland-adapted species (which formed 17% of biomass consumed and 27.90% FO, mainly Egyptian geese, African sacred ibis (*Threskiornis aethiopicus*), and vlei rat (*Otomys irroratus*), and fewer arboreal (biomass: 0.78, FO: 3.97%, mainly grey squirrels, *Sciurus carolinensis*) or terrestrial-adapted species (71.1% biomass, 54.90% FO, such as Guinea fowl, rock hyrax *Procavia capensis,* and four striped grass mouse, *Rhabdomys pumilio*; Appendix 4.10 and 4.11).

iv. Exotic prey group

For PCBs, especially PCB-180 (Appendix 4.12), caracals with a greater proportion of exotic prey biomass (13.80% biomass consumed, 9.85% FO) in diet were significantly more exposed ($\beta = 0.37 \pm 0.19$, $P < 0.1$; Fig. 4.5D). The exotic species that contributed most to biomass consumed were domestic cats and

livestock (i.e., goat and domestic peacock). There were no significant trends in FO models (Appendix 4.13) or with exposure to DDT.

PHYSIOLOGICAL CONDITION AND ORGANOCHLORINE EXPOSURE

Potential physiological responses to Ocs were also investigated by testing for relationships with standard veterinary health blood parameters. White blood cell count, particularly lymphocytes, was elevated in individuals exposed to DDT and PCBs (Appendix 4.14; Fig. 4.7), indicative of an immune system response to infection or disease. Similarly, PCBs, especially PCB-153 and -180, were also correlated strongly with increased WBC count ($\beta = 0.45 \pm 0.22$, $P < 0.05$, Fig. 4.7), indicating this exposure may be triggering the cellular immune response. Further, platelet count was significantly higher when exposed to PCBs ($\beta = 0.24 \pm 0.09$, $P < 0.05$, Appendix 4.14; Fig. 4.7), suggesting a response to potential infection or inflammation (i.e., potentially triggering innate immunologic or inflammatory mechanisms).

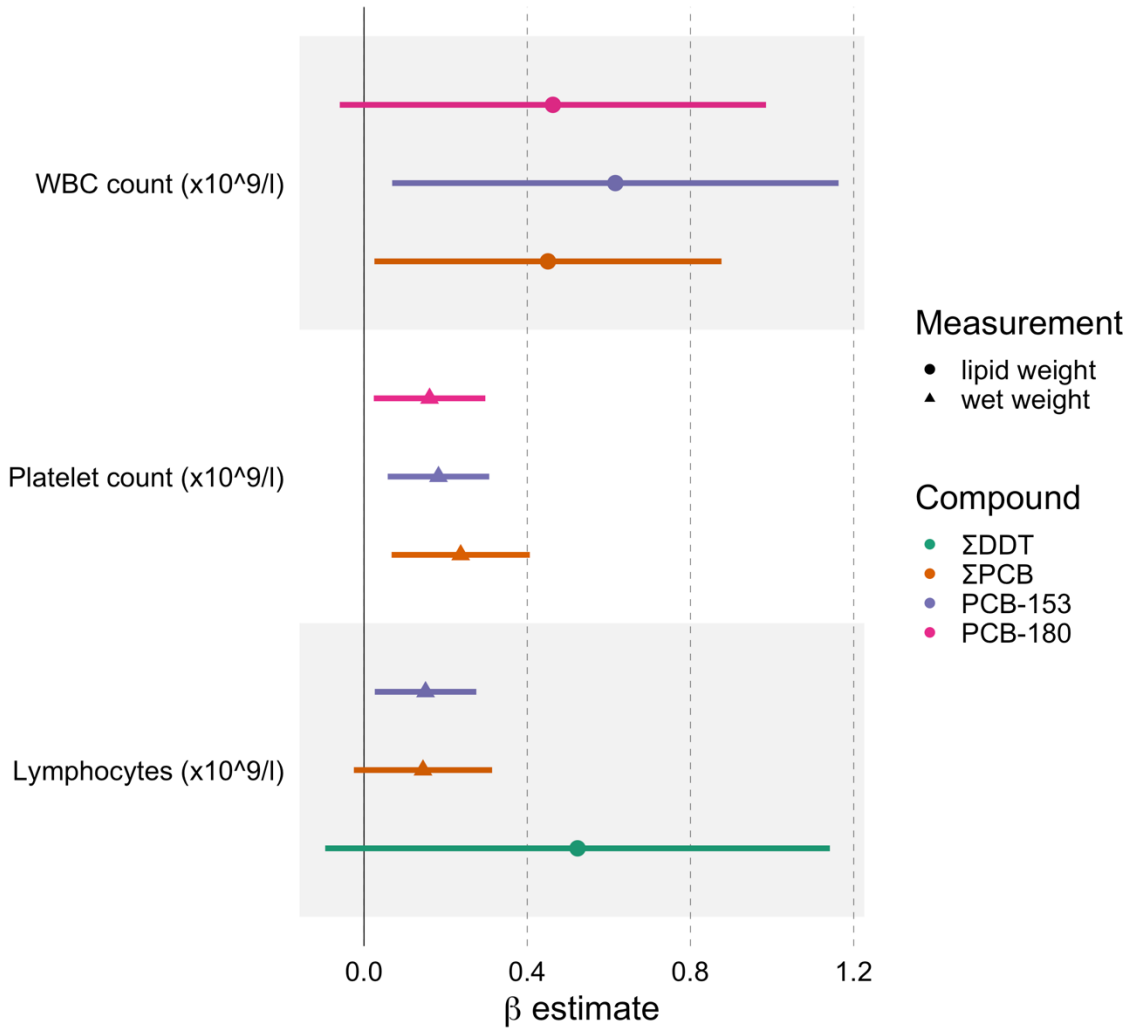


Fig. 4.7 Parameter estimates and 95% confidence intervals for linear models of blood cell count and concentrations of organochlorines in caracal blood in terms of wet (circle) and lipid (triangle) weight. Estimates are shown for those parameters included in the top models (as determined by AICc).

Serum biochemistry models suggest that exposure to Ocs is negatively associated with chlorine (Cl-), potassium (K+), albumin levels and the albumin:globulin ratio (Fig. 4.8), although sample size was limited (i.e., $n < 30$; $n = 23$ w.w., $n = 20$ l.w., Appendix 4.15). There was also some evidence that DDT exposure was negatively associated with creatinine levels ($\beta = -0.89 \pm 0.33$, $P < 0.05$) while PCB exposure was positively associated with urea levels ($\beta = 0.16 \pm 0.07$, $P < 0.05$; Fig. 4.8). However, sample size for these biochemistry models was small, limiting my interpretation of results (Appendix 4.15). There were no significant patterns seen with OC levels and body condition for either the OLS residuals or SMI methods ($p > 0.05$; $w.w._n = 52$, $l.w._n = 48$).

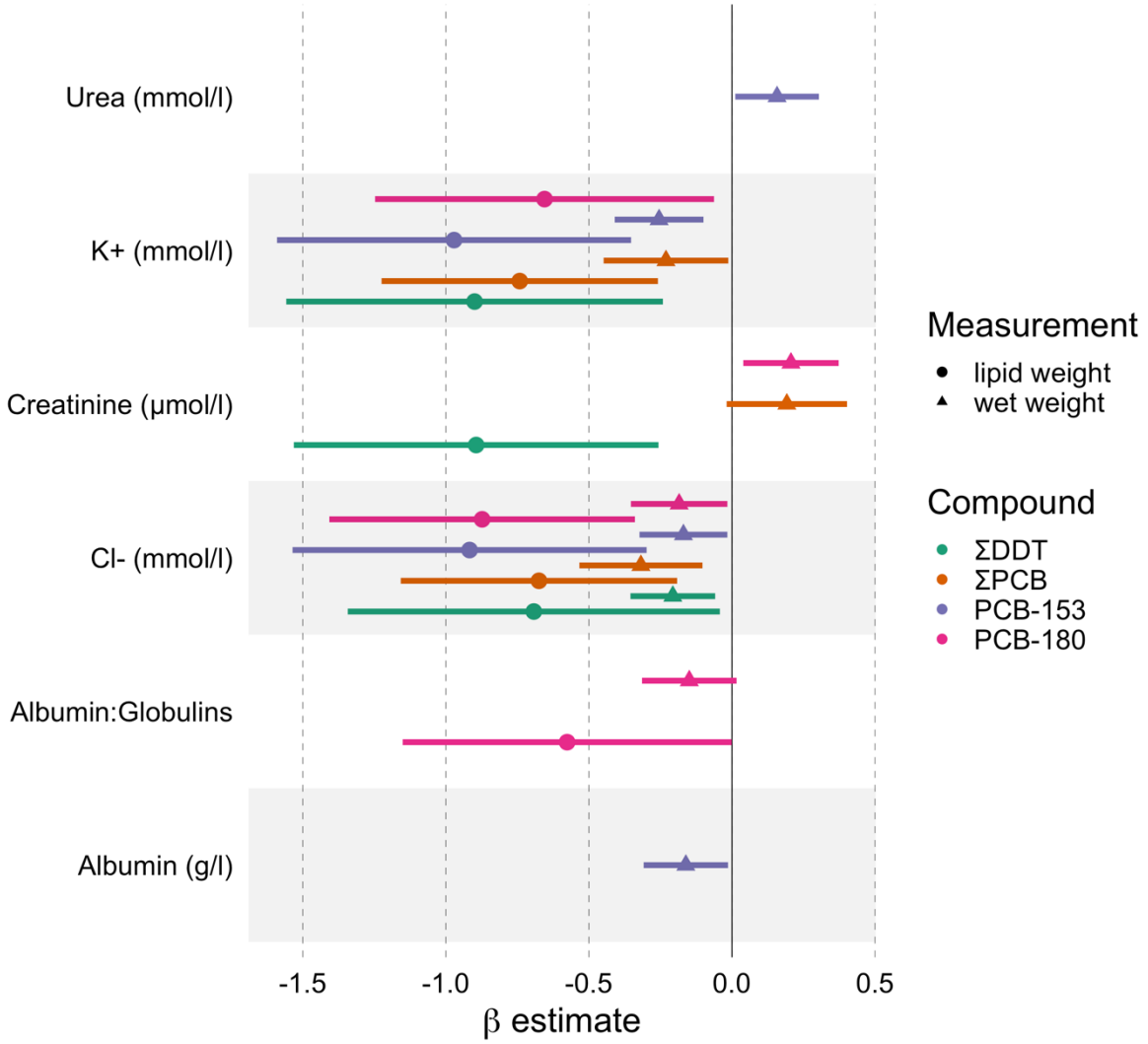


Fig. 4.8 Parameter estimates and 95% confidence intervals for linear models of serum biochemistry and concentrations of organochlorines in caracal blood in terms of wet (circle) and lipid (triangle) weight. Estimates are shown for those parameters included in the top models (as determined by AICc).

DISCUSSION

In this chapter I assessed associations with factors that may drive the accumulation of organochlorines (Ocs), and the consequences of exposure, in the caracal, an adaptable medium-sized felid making use of landscapes in and around the metropolis of Cape Town, South Africa. In this area, caracals have a complex spatial relationship with human-dominated landscapes which depends on demographics and habitat (Serieys et al. *in review*). However, caracals are attracted to forage at the urban edge (Chapter 3; Leighton et al. 2021), where they mainly feed on wild prey but also a significant proportion of human-associated species (Chapter 2; Leighton et al. 2020). As diet can be a major route of exposure to organochlorines (Safe 1994; Dougherty et al. 2000), foraging on human-subsidised prey (i.e., synanthropic and exotic species) close to urbanised landscapes may increase exposure risk for flexible foragers like caracal. My findings reveal extensive population exposure to organochlorines, elucidate multiple potential sources of exposure, and point to potential consequences of exposure. Caracals may therefore serve as excellent indicators for these local contaminants (Corsolini et al. 2000; Dip et al. 2003; Jooste et al. 2013), informing environmental pollutant mitigation and regional conservation efforts. These findings contribute to our global understanding of organochlorine toxicant risks and their contribution to species endangerment in urban areas.

CONTEXTUALISING CARACAL ORGANOCHLORINE LEVELS

Most studies, and consequently our current perspectives, on carnivore exposure to pollutants originate in the Global North (Rodríguez-Estival and Mateo 2019). In this chapter, I augment knowledge on the global patterns in contaminant exposure while contributing to fill the gap in the southern hemisphere, specifically the southern African perspective. There are few studies on environmental pollutants in wild, terrestrial mammalian predators in southern Africa. I discuss my findings where comparisons are possible locally and globally (see Appendix 4.16 and 4.17 for tables of published studies). Unsurprisingly, caracal exposure to Ocs in the study area was higher than ΣPCB levels reported for hyenas (*Hyena brunnea*) and lions (*Panthera leo*) in larger protected reserves elsewhere in South Africa (the Kruger and Addo National Parks), although comparable to ΣDDT in these species (Malarvannan et al. 2020). Caracal organochlorine burden was also comparable to, if not higher than, studies on terrestrial mammalian predators in Europe and North America. For example, ΣPCB and DDT metabolite concentrations in adipose tissue were higher in caracals than in the Endangered (EN; Rodríguez and Calzada 2020) Iberian lynx (*Lynx pardinus*, Spain; Mateo et al. 2012), and in grey wolves (*Canis lupus*) and brown bears in Croatia (*Ursus arctos*; Romanić et al. 2015). Caracal PCB concentrations were also 6 – 15 times higher than in bobcats (*Lynx rufus*) in the state of Illinois, USA (Boyles and Nielsen 2017; Appendix 4.17). Caracal PCB levels were generally lower than those reported to cause

lethality in laboratory mink (*Neovison vison*) but do approach values known to cause reproductive impairment in captivity (e.g., Hornshaw and Aulerich 1983; Kamrin and Ringer 1996). Interestingly, caracals in South Africa have lower OC levels than those reported in mammalian predators from the extreme northern latitudes (Appendix 4.16 and 4.17), which likely experience high levels of exposure through long-range atmospheric transport (Risebrough et al. 1976; Ma et al. 2016). For example, reported PCB levels in Arctic fox (*Vulpes lagopus*) were over 25 times that of caracal levels (Fuglei et al. 2007; Andersen et al. 2015). Similarly, ΣPCB concentrations in subcutaneous lipid of polar bears (*Ursus maritimus*; Bernhoft et al. 1997), liver concentrations in polecats (*Mustela putorius*) from the Netherlands (Leonards et al. 1994), and in wolves from north-west Spain (González-Barros et al. 1997) were far higher than caracals. The data presented here indicates that wildlife around African cities are likely to be exposed to contaminants at a similar level to cities in more developed countries.

Cape Town's human landscapes as a toxic ecological trap

Globally, rapid environmental change centred around urban areas creates cues for novel threats which wildlife may misinterpret, inadvertently leading to poor resource selection via ecological traps and eventual potential population declines (Robertson and Hutto 2006; Smith et al. 2021). In Cape Town, the urban edge may represent a poisoned chalice: caracals increase their exposure to organochlorine pollutants by making use of transformed landscapes to access prey species that persist around urban areas. Caracals may be falling into a trap by actively selecting to forage in habitats, such as vineyards and wetlands, that are suboptimal as they increase their risk of exposure (Remeš 2000; Battin 2004; Lamb et al. 2017). Vineyards in particular are strongly selected as foraging habitat in this area, likely due to easy prey access while still providing adequate cover (Chapter 3; Leighton et al. 2021). This land-use also correlates with higher DDT exposure, most likely pointing to legacy use of this insecticide. Further, the study population of caracals also experiences high anticoagulant rodenticide exposure which was strongly associated with use of vineyards (Serieys et al. 2019). Similar rodenticide exposure caused immune stimulation, increased disease risk and subsequent population declines in bobcats (Serieys et al. 2013, 2015, 2018). Together these studies suggest that vineyards, which are the primary form of agriculture in Cape Town but comprise only a small percentage of the available landscape, may be particularly toxic areas for caracal and other wildlife.

Wetlands near human-dominated areas are transformed by urban and agricultural run-off and effluent from wastewater treatment plants, which is highly nutrient-rich (Brooks et al. 2006; Matthews 2016), potentially attracting diverse and abundant prey species. Wetlands often act as sinks for contaminants, including POPs with low water solubility (Cloutier 2010), and they may therefore represent particularly toxic traps for carnivores foraging near urban or agricultural areas. In Cape Town, rivers and open waterbodies are increasingly polluted and eutrophic (Day et al. 2020). Here, caracals strongly select to forage in areas closer to

wetlands (Chapter 3; Leighton et al. 2021), and use of wetland areas and consumption of wetland-adapted prey species was correlated with DDT and PCB exposure risk. This trend is also reported for *p,p'*-DDE in an avian predator, the Black harrier (*Circus maurus*), a ground-nester and small mammal specialist occurring in nearby nature reserves in the Western Cape of South Africa (Garcia-Heras et al. 2018).

PCBs are highly stable, persistent and lipophilic, and therefore tend to bioaccumulate easily; as a result, and despite bans and restrictions, numerous environmental sources of these contaminants remain (Huang et al. 2007). As carcinogenic and teratogenic neurotoxins, PCBs represent a considerable threat to humans and wildlife (Crinnion 2011; Kania-Korwel and Lehmler 2016). PCBs are not manufactured in South Africa but PCB-containing equipment and PCB commercial mixtures have been imported since the 1930s, mainly for use in the electricity generation sector, where they are still used as insulation fluid in transformers (Ministry of Water and Environmental Affairs 2012). Historic use and broken or leaking electrical equipment could contribute to existing contamination around transformers and substations which are densely clustered around urban and industrial areas (Menad et al. 1998; El-Kady et al. 2007; Gioia et al. 2014). While caracals generally avoid the urban matrix, they do select for areas closer to the urban edge (Chapter 3; Leighton et al. 2021), where density of humans and electrical transformers is higher. When assessing spatial variables linked to urban areas, electrical transformer density was a strong predictor of PCB exposure in caracal adipose tissue. Similar correlations have been reported in Black harriers (Garcia-Heras et al. 2018). Additionally, human population density was a significant predictor for increased PCB-153 levels in blood, and urban area was a predictor for PCB-180 levels in adipose, perhaps pointing to short- and long-term exposure due to multiple human activities in urban areas. At the height of their production from 1930 – 1970, PCBs were primarily used in electrical equipment, but also in many other household products and fixtures (Agency for Toxic Substances and Disease Registry 2000; Rudel et al. 2008; see Table 4.1 for sources). PCB sources affecting wildlife are highly varied and likely include past and/or present household use in addition to industrial activity and electricity generation. Disentangling causative relationships between current and historic sources is clearly very challenging.

Global emission inventories suggest that a major contributor of highly chlorinated PCBs in the atmosphere is uncontrolled or open burning of contaminated products (Breivik et al. 2002). Another strong spatial predictor of long-term DDT and PCB levels in adipose tissue was caracal use of areas peripheral to informal settlements, where burning is a common form of waste disposal, including plastics, rubberised substances and old electrical equipment (Bouwman 2003; Gatari et al. 2005). Additionally, a thriving market for cheap "street pesticides" persists in Cape Town's informal settlements to deal with major rodent and insect pest infestations (Roomaney et al. 2012; Swartz et al. 2018; Buckland and Nattrass 2020). These products can include mixtures of any available agricultural pesticides, which are decanted and sold for domestic use (Rother 2010, 2016). Caracals mainly use wildland areas adjacent to development (Chapter 3; Leighton et al. 2021) and generally had < 1% informal settlement in their used areas, suggesting that routes of

exposure might be via chemical spillover penetrating adjacent wildland and protected areas, including wetlands (Sánchez et al. 2020).

CONSUMPTION OF AVIAN, CARNIVOROUS, AND EXOTIC PREY EXACERBATES POLLUTANT EXPOSURE RISK

Organochlorine burden is also strongly influenced by foraging ecology (Smith et al. 2007; van Drooge et al. 2008; Ortiz-Santaliestra et al. 2015). Generalist species taking advantage of prey near urban areas may be at greater risk of exposure to organochlorines (Dip et al. 2003; Mateo et al. 2012). Further, diet composition can also influence contaminant exposure level (Smith et al. 2007). For example, proportion of birds in diet has been shown to significantly increase pesticide exposure and accumulation in tissues of raptors (Mañosa et al. 2003; van Drooge et al. 2008; Garcia-Heras et al. 2018), but not in all mammalian carnivores studied to date (Mateo et al. 2012). In this chapter, I report that bird biomass in the diet significantly increased PCB but not DDT exposure. Birds may be more exposed to PCBs due to higher vagility allowing them to penetrate deeper into the urban matrix (Smith et al. 2007). Further, birds also have slower metabolism of OCs than mammals, resulting in generally higher rates of bioaccumulation (Walker 1990). Reptiles in diet were also significant positive determinants of organochlorine (DDT) exposure in caracals, which may be attributed to the higher trophic level of their snake and lizard prey (Hoang et al. 2021). Similar results have been shown for reptile consumption in Iberian lynx and other carnivores in Spain (Mateo et al. 2012).

Although there is no data on POP exposure in reptiles around Cape Town, analysis of prey functional groups provides strong evidence for likely POP exposure in reptiles, as individuals feeding on carnivores and insectivores were more exposed to organochlorines. Further, snakes and other smaller mammalian (e.g., large spotted genet, Cape grey mongoose) and avian predators (e.g., spotted eagle owl *Bubo africanus*, rock kestrel *Falco rupicolus*) may be important sources of organochlorines as they are more capable of foraging in the urban matrix and thus bioaccumulating persistent organic pollutants (Gómez-Ramírez et al. 2019; Badry et al. 2020; Hoang et al. 2021). Due to high crime rates (Western Cape Government 2017), Cape Town households commonly have relatively high levels of external security structures (e.g., electric fencing, walls, flood lights), reducing access for larger wildlife species, including caracals. These other, smaller carnivores are therefore more able than caracals to access urban structures, gardens, and roofs, and may be more at risk of organochlorine exposure. These results point to possible tertiary exposure to contaminants, and suggest that ecosystem-wide exposure to environmental pollutants is likely in the study area (Berny 2007). Further, those individuals that feed on exotic prey, including domestic and introduced species, also had higher levels of PCBs. Interestingly, while there were few demographic differences, subadult males had the highest organochlorine burdens in blood DDT levels and PCBs in adipose and blood. This is likely due to higher consumption of human-subsidised prey (both exotic and synanthropic), as well as higher use of urbanised areas with more

electrical transformers and substations. As urbanisation intensifies and wildland areas continue to shrink, the caracal prey base may shift towards more available human-subsidised prey and exacerbate this exposure trend.

CARACALS AS INDICATORS OF POTENTIAL HEALTH IMPACTS

Terrestrial mammalian carnivores are useful ecosystem-level indicators of pollution by harmful toxicants (Jooste et al. 2013). POPs have multiple health impacts on wildlife and humans, including impaired immune system function (Ross and Birnbaum 2003; Sánchez et al. 2020; Sonne et al. 2020). In marine mammals (e.g., Ross et al. 1996; Sonne 2010; Desforges et al. 2017) POPs have well-established immunotoxic effects, causing increased susceptibility to infectious diseases and resulting in elevated bacterial and parasite loads (Wunschmann et al. 2001). Further, energetically costly immune responses to contaminants have population-level implications, as they are linked to reduced reproductive success and fitness (Sonne 2010; Desforges et al. 2016; Dietz et al. 2019). Using caracals as an indicator species, the high risk of organochlorine exposure is revealed for wildlife in both human and wildland landscapes around Cape Town (Fig. 4.4). This accidental exposure may be leading the population into an "ecotoxicological trap" due to health impacts of prolonged exposure to chemical pollutants (e.g., López-Perea and Mateo 2019; López-Perea et al. 2019).

Exposure to organochlorines was positively associated with white blood cell count in caracals, particularly lymphocytes, and increased platelet count, and albumin levels. Specifically, increased lymphocytes signify a potentially elevated adaptive immune response (Desforges et al. 2016). Similar immuno-stimulation has been reported in harbour seals (*Phoca vitulina*) in Canada (Levin et al. 2005) and California, USA (Neale et al. 2005), sea otters (*Enhydra lutris*), three seal species (Mori et al. 2006), and in laboratory rats (e.g., Smialowicz et al. 1989) exposed to OCs. However, this result is in contrast with work on polar bears (Lie et al. 2005), Baltic harbour seals (Ross et al. 1996) and bottlenose dolphins (*Tursiops truncatus;* Lahvis et al. 1995), where OCs are reported to suppress lymphocyte proliferation. This may be because lower concentrations, such as those reported here in caracals, initially stimulate the mammalian cellular immune response, followed by immunosuppressive effects at higher concentrations (Desforges et al. 2017). Interactions of chemical contaminants in differing mixtures may also result in disparate immune responses between species and locations (Vos et al. 2000; Mori et al. 2006; Riley et al. 2014b). However, organochlorines may not be the only cause of such effects in caracals. Importantly, in the study area, habitat features may reflect some activation of the immune function in the animals living in peri-urban areas due to multiple human activities (e.g., through other stress responses or pathogen exposure; Isaksson 2015; Murray et al. 2019), which can complicate elucidating causal relationships. Exposure to other contaminants, such as heavy metals and rodenticides, which have been shown to have population-level effects in other species (e.g., bobcats, Serieys et al. 2015, 2018) may also contribute to immune stimulation. Further work, such as caracal lymphocyte

proliferation testing, is therefore needed to quantify immune responses to OCs, which are often species-specific (Mori et al. 2006; Desforges et al. 2017), as well as testing for other potential stress responses which may be influencing immune status (Isaksson 2010, 2015). Over time, however, even low OC concentrations can cause chronically activated immune responses, which can lead to immune exhaustion and result in increased disease susceptibility and progression (Mori et al. 2006; Sauce et al. 2011; Serieys et al. 2018). Although the smaller sample size available in this study limits interpretation, potential immunotoxicity may become problematic for this caracal population, which is known to be exposed to novel blood pathogens (Viljoen et al. 2020).

There was no evidence of increased organochlorine levels affecting caracal body condition in the study population; therefore, it is likely that these physiological effects may be subtle and sublethal (Berny 2007; Desforges et al. 2016) or alternatively that body condition is an inappropriate metric for OC impacts. Importantly, the findings presented in this study may also have direct implications for the immune function of other local wildlife species, and there is additional cause for concern for impacts on human health through consumption of carnivores too (Domingo 2017). In this study area, opportunistic poaching of caracals and other wildlife for bushmeat consumption has been recorded (Serieys, *unpubl. data*).

MANAGEMENT IMPLICATIONS

Organochlorine contaminants have been banned in South Africa since 2001, but exposure risk could be mitigated by reducing illegal use, particularly through raising awareness and correctly disposing of old equipment and chemical stockpiles. While there is no comprehensive monitoring programme, the state energy supplier, the Electricity Supply Commission of South Africa (Eskom) is currently phasing out PCB-contaminated electrical equipment (> 50 ppm), with over 43 tons destroyed in 2019 alone, and with 79 units currently in the environment (Eskom 2019).

There has been a recorded decrease in DDT concentrations in polyethylene pellets on the country's beaches over the last two decades (Ryan et al. 2012). Yet South Africa still has a major issue with illegal use from stockpiles of obsolete pesticides (Bouwman 2003; Dalvie et al. 2006). Additionally, the current legal use of DDT in malaria areas (in the Northern and Eastern regions of South Africa), where concentrations in pregnant women are the highest in the country (Röllin et al. 2009) and where there is ongoing spillover to wildlife in conservation areas (Wolmarans et al. 2021), likely increases its availability and facilitates illegal use in other regions (Wells and Leonard 2006). Previous attempts to dispose of unwanted pesticides, such as the 1997 South African Department of Agriculture's National Retrieval Project, which retrieved 420 tons of organochlorines, had low public awareness and many subsequent stockpiles were discovered (Naidoo and Buckley 2003; Dalvie et al. 2006). It is clear that organochlorine exposure is a contemporary issue for South African wildlife, justifying the reinstatement of a nationwide pesticide disposal programme, and incentivising

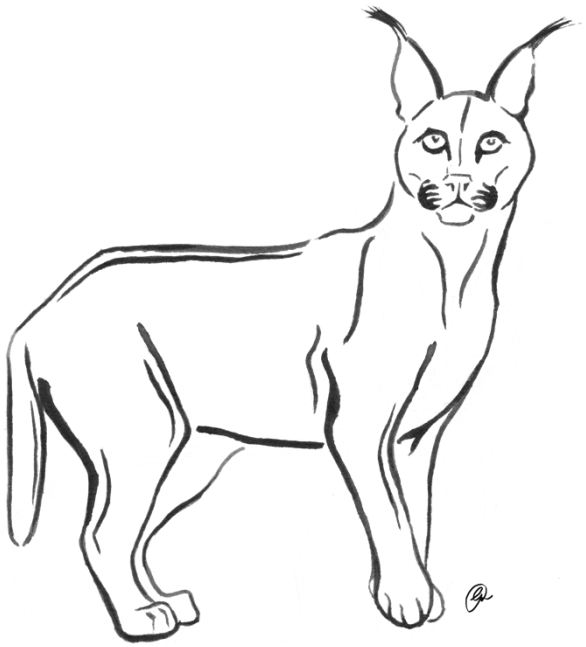
farmers and landowners to catalogue and properly dispose of pesticide stockpiles (Bouwman 2003; Dalvie et al. 2006). Disposal efforts should focus on agricultural areas, particularly those with vineyards, and on informal settlements. Further, wetland clean-up, such as dredging or capping sediments (Agarwal et al. 2007; Cloutier 2010), or bioremediation using microorganisms (Passatore et al. 2014; Mansouri et al. 2017), is necessary to remove organochlorine pollutants in South African urban wetlands.

GLOBAL CONTEXT AND CONCLUSIONS

Globally, wildlife in rapidly urbanising areas are threatened by ongoing habitat transformation and anthropogenic mortality (Hill et al. 2020b). In Cape Town, caracals follow this trend. Overall, my findings point to a mismatch between risk and reward in novel urban ecosystems. In the long term the inability to correctly assess the threat of pollutants may exacerbate wildlife population declines in these rapidly expanding systems (López-Perea et al. 2019; Smith et al. 2021). Mitigating exposure to toxic environmental pollutants and pesticides will therefore be central to the successful conservation of not only this adaptable medium-sized carnivore in this biodiversity hotspot, but all wildlife persisting in transformed landscapes globally. Moreover, my findings likely reflect patterns across other urban and agricultural landscapes in southern Africa. The bioaccumulation of pollutants I document suggests that apex predators, such as leopards (*Panthera pardus*), an IUCN Vulnerable (VU) species (Stein et al. 2020), together with avian predators, will also be secondarily or tertiarily exposed. My results highlight the need to further investigate the health impacts of organochlorines and the potential role of pollutant exposure in species declines. Future research will inform the development of biodiversity conservation priorities and the mitigation strategies needed for population persistence in human-dominated landscapes.

CHAPTER 5

SYNTHESIS



Animals have evolved to make decisions about the potential gains and losses associated with certain activities which have been profoundly disrupted by novel, unpredictable anthropogenic influences. This decoupling of cues for resources and safety can have highly negative consequences for populations experiencing elevated levels of anthropogenic stimuli (Guiden et al. 2019; Smith et al. 2021). It is well-established that carnivores have strong fear responses to human disturbances (risk disturbance hypothesis; Lima and Bednekoff 1999; Frid and Dill 2002), and that proximity to humans and associated habitat disturbances (e.g., logging, roads, urban development), including low impact, benign activities (e.g., recreational hiking), is perceived as risky (Sih et al. 2011; Smith et al. 2015; Oriol-Cotterill et al. 2015b; Clinchy et al. 2016; Nickel et al. 2021). Even the sound of human voices substantially alters carnivore behaviour, making them more cautious and elusive (Smith et al. 2017; Suraci et al. 2019). As a result, carnivores frequently experience displacement by humans both in terms of their ecological role as apex predators (Ordiz et al. 2013; Kuijper et al. 2016), as well as in their spatial and temporal use of human modified landscapes (Gaynor et al. 2019).

Some anthropogenic cues may also be missed or interpreted incorrectly (detection mismatch hypothesis; Smith et al. 2021) by wildlife due to disparity between all associated cues and the sensory capabilities of species (Fisher et al. 2006; Serieys et al. 2015; Meekan et al. 2018). Consequently, wildlife may assign perceived benefit to risky stimuli (e.g., Johnson et al. 2020). For example, animals attracted to human-subsidised food resources may simultaneously increase their vulnerability to harvest, accidental death (Penteriani et al. 2018; Johnson et al. 2020), or exposure to toxicant (Vonesh and Kraus 2009; Ciach and Fröhlich 2013; Savoca et al. 2017; Huang et al. 2018), and ultimately lead to population decline and local extinction (Battin 2004; Lamb et al. 2017). The continued failure to recognise or assess risky cues and maladaptive responses may also increase the likelihood of an under-response to a harmful stimulus (Type II error), resulting in an “ecological trap” for species (Robertson and Hutto 2006). Such “traps” are increasingly common worldwide (Sih et al. 2011; Robertson et al. 2013), where the risk-response mismatch is often overlooked as a link between anthropogenic disturbance and global defaunation and animal declines (Dirzo et al. 2014; Guiden et al. 2019; Smith et al. 2021).

To explore the unique urban trade-offs for an adaptable carnivore, I quantified resource use in caracals by (i) describing diet, (ii) fitting resource selection models, and (iii) assessing the costs for individuals based on their risk of exposure to environmental pollutants linked to urbanisation. Here, I summarise the main findings of my research, provide an overview of factors influencing caracal ecology, ecotoxicology and conservation in a rapidly urbanising landscape, and place these findings in context with similar studies globally.

BENEFITS AND COSTS OF A CATHOLIC DIET

Human activities profoundly alter food webs in and around cities: at the top, large carnivores are removed, potentially facilitating mesopredator release, while at the base, the infusion of anthropogenic sources of food alters the availability, distribution, and nutritional characteristics for consumers (Ryan and Partan 2014). Because urban areas have a variety and abundance of anthropogenic sources of food, behaviourally flexible species which take advantage of these resources should fare best. Animals that incorporate a high proportion of anthropogenic foods into their diets are commonly dietary generalists and omnivores (McKinney 2002; Iossa et al. 2010; Ryan and Partan 2014). For example, in urban areas 14 – 25% of the diet of coyotes (*Canis latrans*) is of anthropogenic origin (Fedriani et al. 2001; Grigione et al. 2011; Larson et al. 2015, 2020), red foxes (*Vulpes vulpes*) over 50% (Contesse et al. 2004; Bateman and Fleming 2012), and large-spotted genets (*Genetta tigrina*) consume up to 13% anthropogenic foods (Widdows and Downs 2015). As with other obligate carnivores, such as bobcats (*Lynx rufus;* Riley 2006; Dunagan et al. 2019), there is less opportunity for caracals to exploit common urban resources such as garbage, pet food, or roadkill (Warren et al. 2006), but they may nevertheless enjoy "secondary resource subsidies" by utilising urban areas to forage on other animals, including pets, livestock, native synanthropes, and non-native invasive species. For example, leopards (*Panthera pardus*) in human-dominated areas in India consume up to 87% anthropogenic prey, particularly domestic dogs and cats (Athreya et al. 2014).

In this study I investigated caracal diet in the rapidly growing city of Cape Town using a novel integrated-diet estimation method that doubled feeding event detection. In doing so I documented the highest prey diversity in any caracal diet study published to date, with over 70 prey species recorded. This dietary breadth may reflect the high biodiversity in the study area (Rebelo et al. 2011; Holmes et al. 2012), as well as the absence of similar-sized competitors and larger carnivores potentially resulting in release from top-down trophic pressure. These findings are consistent with an extreme dietary generalist, as has been reported for this species throughout its distribution (Palmer and Fairall 1988; Mukherjee et al. 2004; Braczkowski et al. 2012; Drouilly et al. 2019), and characterised by their opportunistic use of the most commonly available prey (e.g., Avenant and Nel 2002). However, contrary to expectations, caracals do not appear to benefit overtly from the higher abundance of non-native prey species within urban areas. The results presented here reveal that caracals on the Cape Peninsula clearly prey mainly on wild species with a smaller proportion of synanthropic and exotic prey. Similar results are evident from numerous urban areas around the world where local medium-sized predators predate preferentially on native species despite the availability of non-native prey species. For example, coyotes may actively select natural prey, even among abundant anthropogenic resources (Newsome et al. 2015a), dingoes (*Canis lupus dingo*) in peri-urban areas of Australia consume mainly wild prey (Allen et al. 2016), while bobcats specialise on rabbits (*Sylvilagus* spp.), irrespective of whether they are foraging in wildland or urban areas (Tigas et al. 2002; Riley et al. 2010).

FORAGING IN AN URBAN LANDSCAPE OF FEAR

Increasingly, there is recognition of the human apex predator creating a "landscape of fear" around urban areas (Laundré et al. 2010; Gaynor et al. 2019; Suraci et al. 2019a). As an illustration of this phenomenon, during the recent COVID-19-induced "Anthropause", animals responded to reduced risk of human detection and many species, including carnivores, were sighted in and around cities where they had not been seen before (Rutz et al. 2020; Bates et al. 2021; Silva-Rodríguez et al. 2021). Humans are perceived as threatening and are generally avoided, even by larger carnivores (Frid and Dill 2002; Ordiz et al. 2013; Darimont et al. 2015), but species-specific behavioural plasticity may mitigate the costs of coexisting with increased human activity, either through spatial or temporal partitioning of resources (Oriol-Cotterill et al. 2015b). For carnivores, including felids, near urban areas a trend toward nocturnality has been reported (Gaynor et al. 2018). For example, bobcats take advantage of the general absence of humans to forage in urban areas at night (Tigas et al. 2002; Wang et al. 2015; Dunagan et al. 2019). Peri-urban leopards in India use developed areas (Athreya et al. 2013; Bista et al. 2020) but mitigate overlap with people by approaching the urban matrix only at night (Odden et al. 2014). Similarly, fishing cats (*Prionailurus viverrinus*) in highly urbanised areas of Colombo, Sri Lanka mainly use the urban matrix at night (Ratnayaka et al. *in review*).

When avoidance strategies impact foraging, this can be especially costly to species. For example, pumas (*Puma concolor*) selectively forage at the urban edge, and even change their diet to some degree to do so, but feed for shorter periods or flee when they hear human voices (Smith et al. 2016, 2017). Tigers (*Panthera tigris altaica*) abandon kills more frequently when disturbed by humans (Kerley et al. 2002). Additionally, Eurasian lynx (*Lynx lynx*) reduce their time at kill sites in areas of higher human activity (Belotti et al. 2018). In this study, I investigated caracal fear-based responses while foraging and resting, using the full suite of feeding events in my models, and comparing caracals in an urban-dominated and a wildland-dominated area. Contrary to reported trends, I found that caracals do not exhibit evidence of temporal partitioning of their habitat and are less likely to move off kills, maintaining high fidelity in the urban-dominated region; they also spend longer at feeding sites when nearer to the urban edge in the urban-dominated region. I propose that caracals utilise a specific strategy in response to perceived risk of detection: reducing movement and relying on protective cover and a camouflaged coat to remain hidden, rather than fleeing and abandoning prey. Together, my findings support varied responses by medium-sized carnivores in urban landscapes of fear, and when cover is available, it may be more advantageous for these smaller species to remain cryptic with access to their prey, rather than to incur caloric losses by abandoning them.

My analysis also reveals that levels of exposure to urbanisation strongly affect caracal spatial foraging behaviour. Caracals in the urban-dominated region of the study area focus their foraging activities on the urban edge (Fig. 5.1A and D), and while selection of certain transformed landscapes is identified in the

analysis presented, caracals rarely enter the urban matrix itself. Similar avoidance has been documented for other felids in peri-urban areas. For example, bobcats in California seldom use the urban matrix (Riley et al. 2003; Riley 2006; Dunagan et al. 2019), avoiding high-density housing and rather showing a selection for natural vegetation (Serieys et al. 2021). Bobcats in Texas select for natural and agricultural features and avoid roads (Young et al. 2019a). Jungle cats (*Felis chaus*) remain on the edges of densely populated areas of Bangladesh (Giordano et al. 2018). Additionally, Tsushima leopard cats (*Prionailurus bengalensis euptilura*) living near suburban areas in Japan generally avoid agricultural and residential areas (Oh et al. 2010). In Norway, Eurasian lynx prefer areas with low levels of human-induced habitat modification and avoid more heavily disturbed areas, indicating an ability to coexist in shared landscapes (Bouyer et al. 2015a, b). Adding to this trend, lynx in rural Slovenia avoid human infrastructure and select for high cover when resting (Hočevar et al. 2021), while in low human density areas of the Bohemian Forest along the German-Czech border, they prefer dense vegetation and inaccessible terrain to avoid human activities (Filla et al. 2017; Belotti et al. 2018).

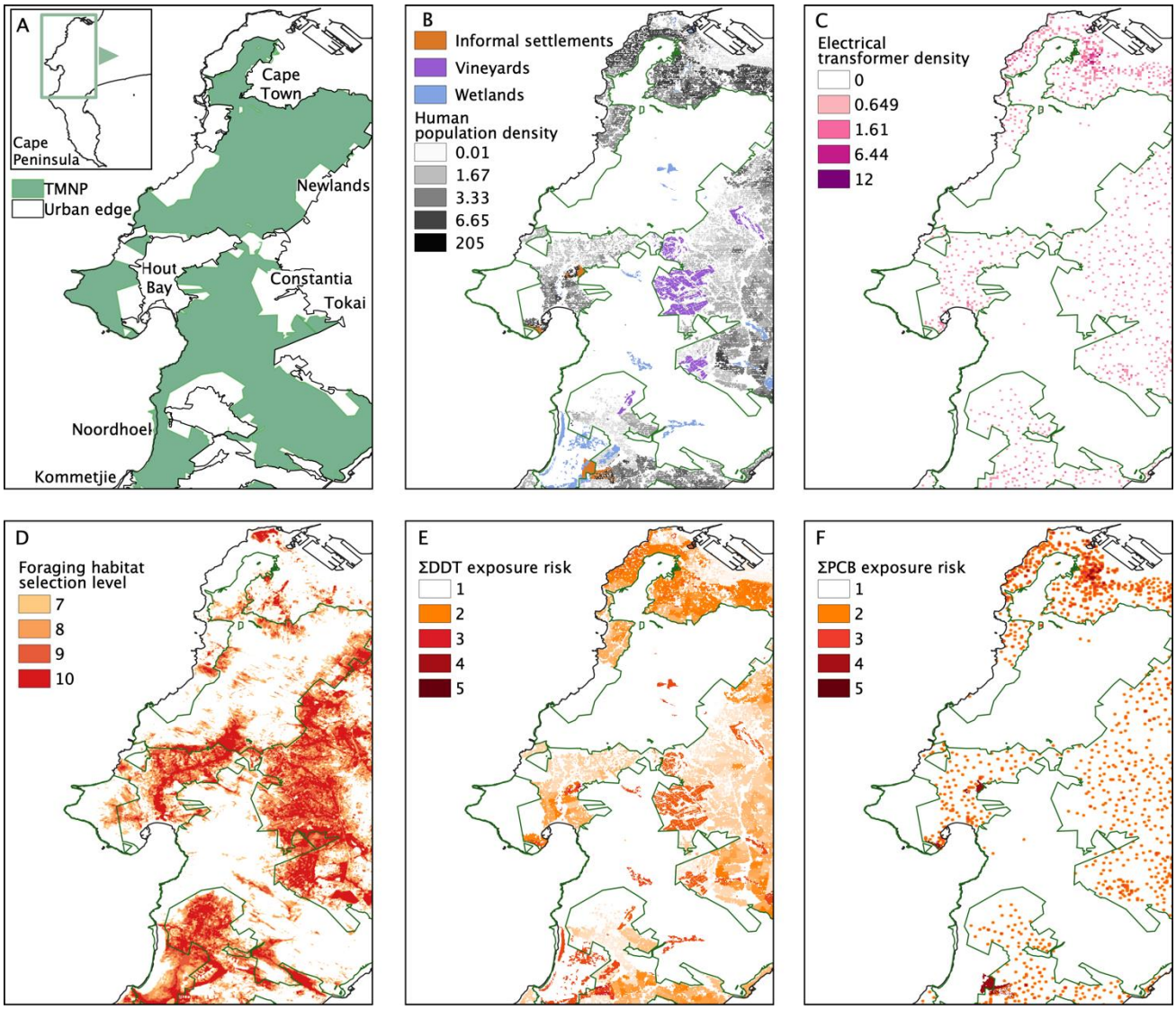


Fig. 5.1 Maps of the urban-dominated, northern region of the Cape Peninsula showing (**A**) Table Mountain National Park (TMNP, in green); relevant spatial variables including (**B**) informal settlements, vineyards, wetlands and human population density (30 m^2) and (**C**) electrical transformer density (100 m^2); selection surfaces for (**D**) the most highly selected foraging areas (corresponding to selection levels 7-10 as presented in Chapter 3, Fig. 3.1); and heatmaps for probability of exposure to (**E**) sum of DDTs and (**F**) sum of PCBs (as presented in Chapter 4, Fig. 4.4).

In contrast to the wildland-dominated region of the study area, caracals in the urban-dominated region select for the urban edge, particularly when foraging in vineyards and in wetland areas, where handling times and fidelity were significantly higher, especially during the day when risk of detection is greater. Here, at the urban edge, where they are faced with urban risk cues and frequent exposure to recreational hikers and cyclists, as well as poachers, they respond not by fleeing, but by hiding: finding vegetative cover where it is available and reducing movement when on a kill by keeping both handling times and fidelity consistently high. Selection for high cover also increases with proximity to the urban edge in the urban region (Fig. 5.2), suggesting the need to hide in place is more important at the urban edge (i.e., when closer to perceived risk). Cape Peninsula caracals overall (both in urban- and wildland-dominated regions) also show a strong positive functional response to the urban edge (i.e., increasing selection with its greater availability on the landscape).

Together, these findings point to a degree of habituation to human disturbance (Fig. 5.3), along with the specific strategy of remaining cryptic.

Fig. 5.2 Untagged juvenile caracal hides behind restios (endemic reed-like plants). Cape Town's caracal rely on vegetative cover to reduce human detection risk and cover is more selected closer to the urban edge where perceived risk is potentially higher. Photograph by C. Meyer, Cape Town (2020).

Trends toward habituation in developed areas have also been documented for other carnivores, such as brown bears (Wheat and Wilmers 2016) and coyotes (Schell et al. 2018). My results suggest that habituation in this study system may alleviate perceived risk and avoidance of human activity, allowing individuals to maximise foraging opportunities. While habituation may lessen some of the impacts of human activity on carnivores, the long-term effects of habituation may nevertheless still be negative, as habituated individuals are likely to be at greater risk of anthropogenic threats (Wheat and Wilmers 2016). Moreover, while individual caracals near urban environments may be more tolerant of humans due to habituation (Mccleery 2009; Wheat and Wilmers 2016; Schell et al. 2018), this trend can be further explained by a degree of selection bias toward animals that have more tolerant or docile temperaments or bold personalities (Martin and Réale 2008; Arroyo et al. 2017; Breck et al. 2019). While the behavioural mechanisms behind tolerance for humans are unlikely to be the same for all species or populations, a consistent trait of "urban-successful" species is that they respond adaptively to the increase in human activity around them (Ryan and Partan 2014).

In addition to improving our understanding of foraging strategies in human-modified landscapes, the results from this study highlight the value of integrating two traditional techniques that together provide a more comprehensive assessment of resource selection in a medium-sized carnivore. Although new technologies to detect feeding events of small prey are being developed, such as the use of accelerometers and microphones to recognise periods of stalking, chasing and chewing (Studd et al. 2021), these approaches remain very expensive for field applications, and still preclude recording micromammal and invertebrate prey (e.g., insects).

Fig. 5.3 Photographs of TMC33 Hermes, an adult male caracal who was hit by a car in 2018 but tagged and released (see http://www.urbancaracal.org/meet-the-cats), that show his remarkable habituation to people and human structures. TMC33 is frequently sighted within Table Mountain National Park by tourists, hikers, mountain bikers and trail runners. Photographs by (**A**) G. Myata in 2019, (**B**) F. Sacks in 2020, (**C**) Y. Tromp in 2019 and (**D**) M. Pan in 2019.

THE DANGERS OF PERI-URBAN FORAGING

The long-term environmental impacts surrounding the use of dichlorodiphenyltrichloro-ethane (DDT) and its analogues raised public and government awareness of the environmental and societal costs associated with synthetic chemicals used in the management of agricultural and public health pests (Carson 1962; Riley et al. 2014b). In addition, there has been a move to understand the linkages between the health of humans and ecosystems through the "Global One Health Paradigm" (Kahn et al. 2009; Gebreyes et al. 2014). Currently, there are restrictions to the sale and use of persistent organic pollutants (POPs), including many toxic pesticides and other synthetic compounds (e.g., Stockholm Convention, 2001). However, due to legacy contaminants (i.e., those no longer used in industry but that remain in the environment, such as DDT, which has a half-life of up to 15 years) and ongoing illegal use of banned chemicals, wildlife continue to be negatively impacted by POPs, particularly those species in urban areas (Riley et al. 2014b). It is widely reported that POPs, including organochlorines, such as polychlorinated biphenyls (PCBs) and DDT and its metabolites, are extremely toxic, causing adverse effects on wildlife and human health (Ross and Birnbaum 2003; Ortiz-Santaliestra et al. 2015; Sonne et al. 2020). In this study I used an ecotoxicological approach to assess the wildlife exposure to these environmental contaminants in the city of Cape Town. I used a mixed model method to determine the spatial correlates of exposure and investigated potential health consequences of caracal peri-urban foraging. I tested tissues of caracals utilising differing landscapes and foraging habits for exposure to commonly detected persistent organic pollutants (POPs). Despite strict restrictions, I found extensive organochlorine burdens, with 100% of adipose samples exposed to both DDT and PCBs, and 100% and 83% of blood samples exposed to PCBs and DDT. Similar results and comparable levels have been reported for tissues of carnivores in the Global North, including felids, such as Iberian lynx in Spain (*Lynx pardinus*; Mateo et al. 2012), bobcats in the state of Illinois, USA (Boyles and Nielsen 2017), Florida panthers, USA (*Puma concolor coryi*; Facemire et al. 1995), and in hair samples of leopard cats (*Prionailurus bengalensis*; Iatrou et al. 2019) and eight wild cat species in Iran, including caracals (Dahmardeh Behrooz et al. 2020).

I found that when caracals increased their use of human-modified areas, such as those with higher human population and electrical transformer density and high-density informal settlements, this was strongly associated with increased exposure to OCs. Similar results have been found for use of transformed areas by raptors (Garcia-Heras et al. 2018; Gómez-Ramírez et al. 2019; Buck et al. 2020). Alarmingly, highly sought-after hunting grounds for caracals, such as vineyards and wetlands, are also areas significantly associated with increased risk of exposure to organochlorine pollutants (Fig. 5.1D – F). Further, exposure risk was higher in individuals feeding on higher trophic level prey species, and on exotic prey (e.g., domestic cats and introduced rodents). These findings point to bioaccumulation of OC toxicants and therefore the likelihood of widespread exposure across local food webs (Fig. 5.4). Additionally, this study emphasises the importance of detailed

dietary data for improved understanding of behaviour-explicit landscape use and ecotoxicological pathways through prey.

I also found that increased exposure to OCs may be associated with established physiological effects, indicated by strong correlates with counts of infection-fighting cells, suggesting these compounds may impact on the immune response of caracals and possibly influence their susceptibility to disease. With time, these detrimental effects may have population-level repercussions through impacts on reproductive success and fitness. Similar concerns have been raised for the endangered Florida panther, where environmental contaminants, including *p,p*'-DDE and PCBs, may be a major contributor to reproductive impairment in a previously isolated and inbred population (Facemire et al. 1995).

Overall, these findings point to a potential ecological trap scenario, where caracals are not able to perceive and detect the risk of consuming contaminated prey but are attracted to forage in transformed landscapes where this risk is higher (i.e., evidence for the detection mismatch hypothesis; Fig. 5.1 and Fig. 5.4). Similar ecotoxicological trap scenarios have been proposed and investigated for otters (Delibes et al. 2009; Okes 2017; Huang et al. 2018) and mink (*Mustela vison*; Beckett et al. 2005; Bursian et al. 2013) using polluted harbours and river systems. These results also have implications for human health. There is increasing evidence that both humans and wildlife share pollutant exposure pathways, and that terrestrial carnivores can function as general indicator species (Colborn et al. 1993; Corsolini et al. 2000; Ross and Birnbaum 2003; Jooste et al. 2013). The continued human use of these compounds in informal settlements carries the risk of potential direct exposure (Rother 2010, 2016) and additional exposure may take place through contaminated sites in vineyards and wetlands. Further, human secondary and tertiary exposure may occur due to occasional poaching and bushmeat consumption of both caracals and their prey exposed to various pollutants in the study system.

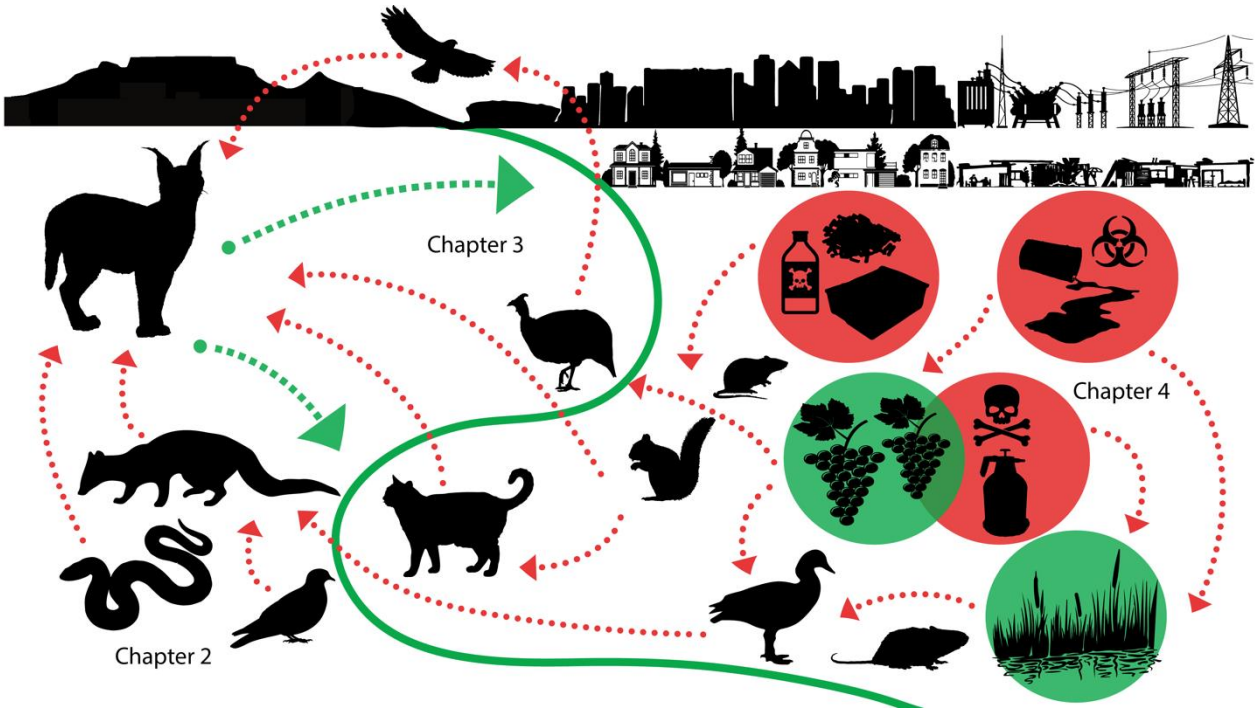


Fig. 5.4 Cape Town's human landscapes as an ecotoxicological trap. Green areas are attractive to caracals for foraging (the urban edge, vineyards, and wetlands). Green dashed lines indicate selection for the urban edge. Red areas are identified potential sources of environmental pollutants (household/informal settlement use of pesticides and PCB-containing products, leakage from electrical equipment and agricultural use of pesticides, particularly in vineyards). Red dotted lines indicate likely pathways of exposure for caracals and their prey.

MANAGEMENT AND THREAT MITIGATION RECOMMENDATIONS

The Anthropocene heralds a new age of ecosystems adversely impacted by human influences (Dirzo et al. 2014). In light of the ongoing pandemic (Bonilla-Aldana et al. 2020), it is evident that human health and wellbeing are inextricably linked to ecosystem health (Gebreyes et al. 2014). Conservation efforts that aim to ensure functioning ecosystems within and adjacent to rapidly developing areas go beyond the importance of conserving wildlife, as there are direct associated benefits for people, too (Shwartz et al. 2014). As a charismatic species with large resource requirements, caracals are important as both umbrella and indicator species (see Fig. 5.4; Sergio et al. 2006; Jooste et al. 2013). Understanding how caracals adapt to living and foraging in an isolated, fragmented national park surrounded by urban areas and the substantial threats they face, has benefits beyond local single-species conservation targets.

In functionally closed populations, a suite of conservation interventions is essential to ensuring population viability and resilience in the face of the diverse negative impacts associated with transformed landscapes. Complex threats to wildlife, such as pollution and poaching around informal settlements, are very challenging for conservation authorities to resolve, and require a transversal approach that cuts across many different government and societal sectors, including the need to address the root societal issues of poverty

and joblessness (Goodness and Anderson 2013; Manaliyo 2014; Pan et al. 2015). Further, the varied stakeholders surrounding an urban park hinder decisive conservation action (Graham and Ernstson 2012; Nattrass and O'Riain 2020). The adaptive management of wildlife in and around cities is also fraught with controversy linked to divergent world views of how people perceive wildlife and their rights relative to people (Patterson et al. 2003; Dickman 2010). In Cape Town, conservation authorities, animal rights activists, the general public, scientists, and NGOs are invariably at odds with each other to some degree when tackling how best to manage wildlife in such a disrupted ecosystem (Goodness and Anderson 2013; Engelbrecht et al. 2017; Nattrass and O'Riain 2020). These complexities are very well portrayed in the highly polemic discussions regarding the management of the Peninsula's chacma baboon (*Papio ursinus*) population (Hurn 2011; O'Riain 2015), white sharks (*Carcharodon carcharias;* Engelbrecht et al. 2017) and, to date, unsuccessful attempts to manage "problem" caracal individuals around Cape Town (Nattrass and O'Riain 2020). As opportunistic carnivores that adapt well to feeding on any available prey, including IUCN Endangered (EN) seabirds (e.g., African penguin, *Spheniscus demersus* [Birdlife International 2020], and Cape cormorant, *Phalacrocorax capensis* [Birdlife International 2018]) and pets (e.g., domestic cats), there is a clear need for management interventions, yet there is also little effort to develop science-based, sustainable and transparent conservation action plans, and limited opportunities for public engagement (Nattrass and O'Riain 2020).

Worldwide, only small, fragmented areas of the historic range of many carnivores are currently protected (Crooks et al. 2011). "Land sparing" is thus a priority for managing carnivores (López-Bao et al. 2017), particularly for the establishment and protection of corridors connecting intact wildland habitat patches (Hofmann et al. 2021). In developing areas where the remaining wildland is shrinking and fragmenting at an alarming rate, it is essential that urban planning reflects and protects the ecological needs of the remaining wildlife (Holmes et al. 2012; Goodness and Anderson 2013). Restoration of urban biodiversity is already in many instances the only option for meeting conservation goals in cities like Cape Town (Goodness and Anderson 2013). Here, priority should be given to restoring and maintaining connectivity between sections of Table Mountain National Park that have been isolated by urban developments, particularly over the past 25 years (Goodness and Anderson 2013). This is particularly important for corridors between important caracal foraging areas (e.g., low lying areas with wetlands, such as Noordhoek, and coastal sites with access from wildland areas, such as Kommetjie; see Fig. 5.1A) and restoring less selected areas to natural fynbos vegetation (e.g., pine plantations within TMNP in Hout Bay, Constantia, Tokai, and Newlands; see Fig. 5.1A). While caracals do show selection of some transformed areas (e.g., vineyards and altered-open areas) where prey may be locally abundant (Fig. 5.1B and D), I demonstrate in Chapter 4 that this may result in higher levels of exposure to pollutants. Thus, improved connectivity and restoration of wildland habitat needs to be prioritised alongside strategies aimed at reducing environmental pollution, particularly along the urban edge.

Although caracals appear to have, in part, habituated to urban areas and even to people utilising the landscapes of TMNP (Fig. 5.3), the results presented here reveal that when they have less exposure to urbanisation (e.g., in the southern section of the Peninsula which has large tracts of wildland habitat), caracals generally avoid the urban edge. Furthermore, when caracals encounter urban areas through loss of low-lying land and selection of the urban edge, as is the case for the northern section of the Peninsula, they nevertheless adjust their foraging behaviour to reduce detection. Selecting to forage and move along the urban edge exposes caracals to densely populated residential areas with a large road network. It is perhaps not surprising therefore that vehicle collisions are the major cause of direct mortality (Fig. 5.5; L. Serieys*, unpubl. data*), with environmental pollutants associated with urban development being a potentially major indirect threat to caracals. Because both caracal collisions with vehicles and exposure to pollutants are spatially non-random (Chapter 4; Serieys et al.*, unpubl. data*), it is possible to implement focused intervention efforts. Thus, signage, wildlife warning reflectors and traffic calming devices (Benten et al. 2018) can all be used to reduce vehicle collisions in caracal-vehicle collision hotspots, particularly those along Cape Town's M3 highway, Ou Kaapse Weg, Glencairn Expressway and Camps Bay Road. Longer term measures, including wildlife crossings such as tunnels or bridges, although expensive to retrofit, should also be considered (Corlatti et al. 2009; Glista et al. 2009; Beben 2012). Felids, such as pumas, are known to use underpasses (Clevenger and Waltho 2005). In southern Florida, the endangered Florida panther and bobcats both use underpasses on the Interstate 75 specifically constructed for wildlife crossings (Foster and Humphrey 1995). Bobcats and pumas are also documented using road bridges and culverts to cross busy roads (Riley et al. 2014a; Serieys et al. 2021).

As for other carnivores, it is unlikely that caracals perceive, assess, and therefore avoid the risk of contaminated prey. Despite the international restrictions and limitations on organochlorines (OCs) by the Stockholm Convention (Lallas 2001), national prohibitions on PCBs (DEA 2014) and highly restricted legal use of DDT in South Africa (Wells and Leonard 2006), I found widespread exposure to these toxic contaminants in Cape Town's caracals, as has been shown in other wild felids (e.g., Florida panther, Facemire et al. 1995; Iberian lynx, Mateo et al. 2012; bobcats in Illinois, USA, Boyles and Nielsen 2017). Therefore, to alleviate the threat of toxicants both industry and government must attempt to reduce pollution of important caracal foraging areas. For reducing illegal access to organochlorines and off-label use of pesticides, an agricultural pesticide retrieval programme on local and national levels should be instigated. Further, awareness and education programs around the correct disposal of old electrical equipment and PCB-containing household products may reduce spillover (Riley et al. 2014b). As sinks of contaminants, there should be a clear focus on the clean-up of Cape Town's wetlands, along with continued monitoring of levels (Wolmarans et al. 2021). In terms of other known pollutants that affect the population, such as rodenticides (Serieys et al. 2019), threats can be reduced by stipulating improved waste management to reduce rodent access to food resources, banning the most toxic rat poison compounds, or at least making them less accessible in shops and

accompanying them with suitable warnings. For example, work on bobcats in southern California was used to develop new regulations that limit the application and sale of second-generation anticoagulant rodenticides, such as brodifacoum and bromadiolone (Riley et al. 2014b; Serieys et al. 2015).

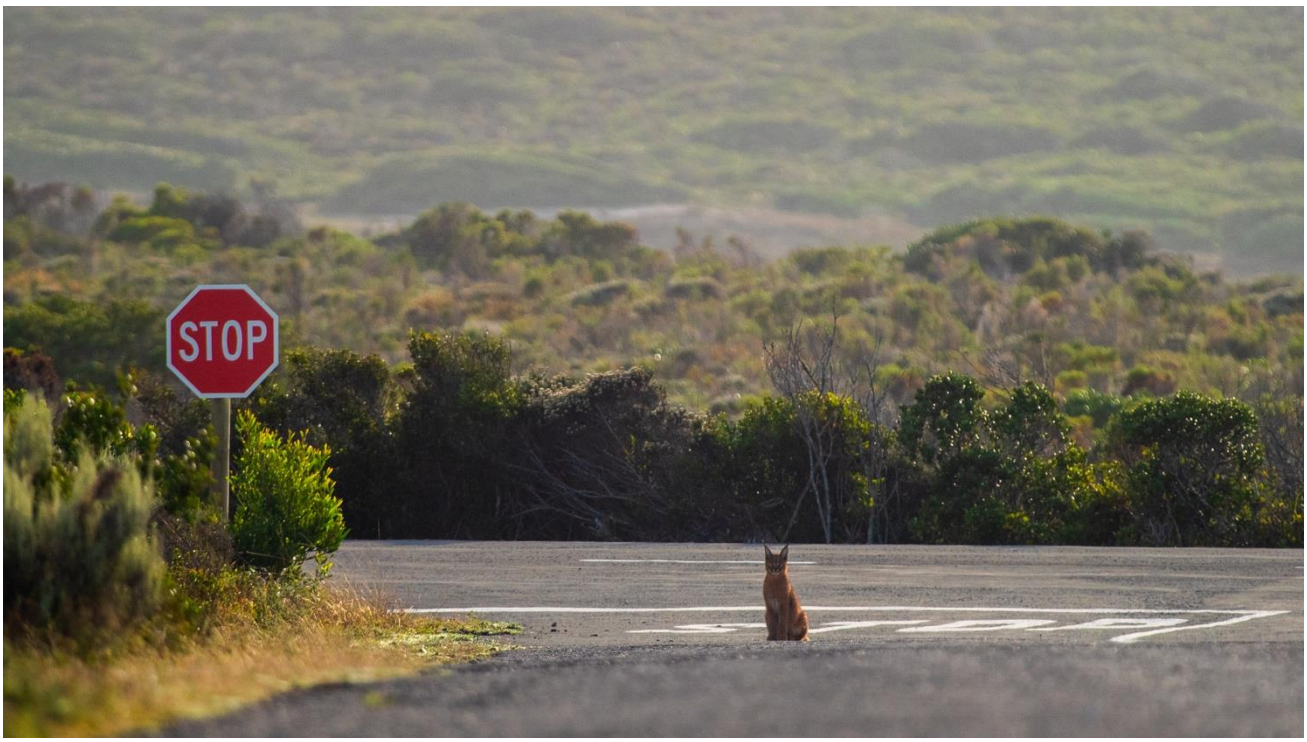


Fig. 5.5 Untagged juvenile caracal sitting on the road near a stop sign in Cape Point nature reserve in the southern Peninsula. The greatest cause of mortality for Cape Peninsula caracals is vehicle collisions. Photograph by L. Nelson (2020).

Attempts could also be made to realign anthropogenic stimuli and risk perception (Smith et al. 2021) in areas of known conflict around Cape Town, such as the Boulders Beach African penguin colony and in eco-estates (Nattrass and O'Riain 2020) where "problem individuals" (i.e., a conflict-causing animal) have been identified. For example, using fear conditioning (Petracca et al. 2019; Young et al. 2019b) to train caracals to associate humans and their settlements with risk could lessen this conflict. Although expensive, combining this approach with predator-proof fencing to reduce access to extremely sensitive areas, such as breeding colonies of endangered seabirds, may result in a more sustainable management solution (Fehlmann et al. 2020). Additionally, while not a major component of their diet, raising awareness around predation risks to domestic animals and livestock on the urban edge (i.e., keeping indoors or in enclosures at night) could further reduce both the perceived and real negative impacts of caracals in urban areas.

Overall, the results presented in this thesis allow for both urban and protected area conservation authorities to identify risks to caracals and stimulate the development of management options to mitigate them. Addressing these threats will, of course, benefit other wildlife species on the Peninsula that face similar threats, including otters (*Aonyx capensis*) and baboons, which have both been shown to be at risk from

vehicles, people and pollutants (Hoffman and O'Riain 2012; Okes 2017). To address specific conservation needs, management task teams have been formed for other felids species globally. For example, in the USA there are state-specific Bobcat Management Plans, in Europe there is the Action Plan for the Conservation of the Eurasian Lynx (Ozoliņš et al. 2017), and the Iberian Lynx Ex situ Conservation Programme that seeks to establish new free-ranging populations using re-introduction programmes through a managed captive population (lynxexsitu.es/programa-en.php). Establishing a joint task team, as has been done for the management of baboons, may facilitate the realisation of coordinated management interventions, given that caracals and other wildlife readily traverse land owned and/or managed by national, provincial, private, and civic authorities. A management action plan could therefore be developed by this team for caracals on the Peninsula, as done for other species requiring focused conservation efforts in South Africa (e.g., white sharks [DAFF 2013], African lion [*Panthera leo*; Funston and Levendal 2015], African elephants [*Loxodonta africana*; SANParks 2012], African penguin [DEA 2013], and Cape Mountain zebra [*Equus zebra zebra*; Birss et al. 2018]).

FUTURE RESEARCH

To further understand how caracals may benefit or be harmed by foraging within or close to a large city there are several possible avenues for future research. Firstly, a rigorous assessment of prey distribution and abundance, beyond the scope of this study, is essential for understanding the selective consumption of urban-associated prey at the urban edge, in addition to whether the most commonly consumed prey items (i.e., Guinea fowl *Numida meleagris*, Egyptian geese *Alopochen aegyptiaca*, Cape cormorant, vlei rats *Otomys irroratus*, and rock hyrax *Procavia capensis*) are simply more abundant. Additionally, with estimates of prey numbers across the urban gradient, it may be possible to determine whether abundance of food resources acts to partly buffer caracals from the detrimental effects of stress from human-related activities or infection from the many diseases prevalent in domestic animals in this area (Suri et al. 2017). Further, estimates of resource use can be improved by DNA barcoding identification of prey items in scat (Morin et al. 2019) and to identify the source individual caracal (Taberlet et al. 1999; Farrell et al. 2000; Adams and Waits 2007). This can be complemented by non-invasive stable isotope analysis of diet to compare patterns of assimilated resources over a larger spatial scale (Hopkins et al. 2014; Newsome et al. 2015a).

To better understand the ecotoxicological threat to Cape Town's faunal biodiversity as well as its human population, further toxicant testing should be undertaken. Testing of prey items, especially other carnivores (e.g., Cape grey mongoose, *Galerella pulverulenta*, water mongoose, *Atilax paludinosus*, large spotted genet, raptors, and snakes) for exposure to organochlorines across the urban gradient will aid in substantiating exposure routes. Combined with prey abundance data across the urban gradient, this information will also provide further details on whether caracals generally prefer habitats with more contaminated prey. Additional

testing should also be performed for other common urban-associated pollutants (e.g., organohalogens, PBDEs, PFCs, and heavy metals) and their spatial correlates analysed. For example, both heavy metal and organochlorine exposure were examined in Iberian lynx (Millán et al. 2008; Mateo et al. 2012), wolves in Russia (Shore et al. 2001) and Bonelli's eagles (*Aquila fasciata*) in Spain (Ortiz-Santaliestra et al. 2015). This added analysis will add to our understanding of the adverse effects of the exposure to mixtures of multiple contaminants (e.g., metals and organic pollutants), especially in urban areas where such a diverse array of chemicals are used (Vos et al. 2000; Riley et al. 2014b).

To further explore the risk of an ecological trap for Cape Town's caracal, it is necessary to provide causative evidence of the relationship between increased levels of pollutants and clear fitness effects and population decline (Robertson and Hutto 2006; Hale and Swearer 2016). The detrimental impacts of being attracted to areas where exposure to contaminated prey is more likely could be further assessed by linking exposure with other stress and health measures, and testing whether these measures vary in habitats with and without contaminated prey. For instance, the link between exposure and health effects through immunotoxicity could be further evaluated by testing caracal-specific functional immune assays (lymphocyte proliferation, phagocytosis, respiratory burst, and natural killer cell activity), immunoglobulin production, and cytokine gene expression (Desforges et al. 2016). Moreover, to disentangle whether the health impacts of foraging at the urban edge are due to pollutant exposure or to stress, or a combination of both, further testing is needed. This could be achieved by assessing stress hormones in caracals, such as glucocorticoids (Sheriff et al. 2011) and cortisol (Macbeth et al. 2010), or oxidative stress, using biomarkers of antioxidants and DNA damage (Isaksson 2010, 2015), across a gradient of urbanisation and linking this to immune responses.

Future research focused on a better understanding of wildlife behavioural adjustments to human disturbance would be of value to conservation efforts in transformed landscapes. Despite numerous examples of apparent risk-response mismatch in wildlife, it is often challenging to assess perception of risk in wild animals, especially in complex urban systems (Gaynor et al. 2019; Smith et al. 2021). Going forward, a valuable research focus would be how these responses to risk scale up to affect individual behaviour and predator-prey interactions at the landscape level (Smith et al. 2020b). Understanding the cues that caracals and other carnivores respond to, and what they perceive as risky, can provide valuable insight, and inform evidence-based conservation strategies to mitigate costly avoidance behaviours or conflict with humans. For example, experimental exposure of anthropogenic cues to animals across disturbance and environmental gradients may elucidate the mechanisms of behavioural responses and to investigate when and how risk-response mismatches occur (Smith et al. 2020a). Specifically, using experimental camera-trap applications to set up playback experiments with video at cluster-identified feeding sites to test responses to human noises (Smith et al. 2017, 2020b). This work will deepen our understanding of both carnivore risk perception and risk-mitigation strategies in human-transformed landscapes.

CONCLUSIONS

As wild areas are increasingly transformed and fragmented, resident wildlife species are forced to share space with humans (Venter et al. 2016). Urban areas have complex outcomes for wildlife where risk and reward may play out differently depending on a combination of phenotypic and behavioural flexibility, susceptibility to threats and risk perception (Kark et al. 2007; Lowry et al. 2013), and where most species exhibit differing responses to human disturbance (Nickel et al. 2020; Suraci et al. 2021). This study represents the largest GPS-collaring and feeding site investigation effort for caracals yet, and takes a novel, integrated approach to evaluating diet, resource selection and costs in a rapidly urbanising area. The findings presented here demonstrate that this adaptable carnivore successfully exploits transformed landscapes for foraging opportunities, showing remarkable behavioural flexibility and ability to habituate to anthropogenic risk cues in order to take advantage of resources at the urban edge. This study therefore affords exciting insight into some of the risk mitigation strategies employed by wildlife using transformed landscapes, particularly the unique behavioural adaptions of cryptic medium-sized carnivores that facilitate their coexistence in close proximity to humans.

Positioning the caracal as an indicator species for exposure to organochlorine pollutants for the first time, this study identifies critical foraging areas and hotspots of toxicant risk in the surrounds of Cape Town, which often overlap. I argue that Cape Town's urban fringes represent an ecotoxicological trap for caracal as a result of their risk detection mismatch, which also threatens the health and long-term persistence of other wildlife in this biodiversity hotspot. While caracals are currently classified as least concern (LC) throughout their range by the IUCN (Avenant et al. 2016), they may not remain so locally, and certainly may disappear from the Cape Peninsula if we are complacent about reducing pollutant exposure risk, geographic isolation and other threats. The implications of the findings presented here extend far beyond the study system, as similar trap scenarios are demonstrated to threaten the persistence of wildlife in polluted areas globally. As urban areas continue to expand and these ecological traps become more common, they will require focused mitigative action. Conservationists must do more to understand how adaptable species successfully navigate increasingly transformed landscapes, and to reduce anthropogenic causes of population decline. Finding ways to protect, sustain, and engender coexistence with species remaining in human-modified landscapes will be essential to modern conservation efforts.

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LIST OF TABLES

LIST OF FIGURES

Fig. 2.7 Rank abundance plots for prey items identified to species level per GPS cluster with prey remains (n=296) and per scat (n = 590). Helmeted guinea fowl (*Numida meleagris*), Cape cormorant (*Phalacrocorax capensis*) and Egyptian goose (*Alopochen aegyptiaca*) were the most dominant species for prey remains. Vlei rat (*Otomys irroratus*), Cape cormorant and Rock hyrax (*Procavia capensis*) were the dominant species present in scat.

Fig. 2.8 Boxplots (median, interquartile range, and upper and lower quartile; diamonds = means) of estimated caracal prey biomass (kg, log-transformed) using GPS cluster analysis for three fix rates (3-hour, 20-minute and clusters formed using both fix rates) of collared caracal (n = 22) on the Cape Peninsula, Western Cape, South Africa. Letters indicate significant differences determined by post-hoc Tukey HSD tests.

Fig. 3.1 Cape Peninsula study area showing (A) feeding clusters (circles, n = 326), back-traced scats feeding events (triangles, n = 384) and resting beds (crosses, n = 117), and (B) selection surface for urban-dominated and wildland-dominated regions with estimates based on the top land-use integrated-diet (scaled) RSF models. Higher values indicate stronger positive selection.

Fig. 3.2 Cape Peninsula study area showing home ranges (95% LoCoH-*a* isopleths) for male and female caracals (n = 17) considered when measuring availability (third-order selection; see *Methods*) for resource selection analysis.

Fig. 3.3 Continuous parameter estimates and 95% confidence intervals based on standard errors for RSFs (logit scale). Estimates are shown for those parameters included in the top models (as determined by AICc) for the urban-dominated (orange) and wildland-dominated (green) regions. *Feeding clusters* (circles) is the GPS cluster prey remains dataset; *integrated-diet* (triangles) is the dataset with both cluster prey remains and scats. *Note that negative distance values indicate selection for habitat closer to the feature.

Fig. 3.4 Probability of a caracal selecting habitat given distance to the urban edge based on RSFs for, (A) caracals in both urban- and wildland-dominated regions and (B) urban-dominated region caracals for different land-uses, (C) at different levels of cover in the urban-dominated region for the scaled integrated-diet dataset (i.e., feeding events from both GPS cluster prey remains and scat, see *Methods*). The 95% confidence intervals are based on standard errors. Note that axes differ between plots.

Fig 3.5. Functional response by (A) all caracals and (B) only caracals in the urban-dominated region of the Cape Peninsula, South Africa, relative to urban edge. Functional response is exhibited by the relationship between a selection proportion for the urban edge and the mean distance to the urban edge across each home range. Proportions of 0.5 represented no difference between used and available, whereas proportions < 0.5 indicated caracals were closer to the urban edge than expected, and proportions > 0.5 indicated caracals were further from the urban edge than expected.

Fig. 3.6 Caracal feeding cluster variables against distance from the urban edge between diel periods: (A) degree of cover measured *in situ* at clusters (B) handling time in the wildland-dominated region (C) cluster fidelity in the wildland-dominated region of the Cape Peninsula, South Africa. Note that axes differ between plots.

Fig. 4.1 Map showing locations of individual caracal sampled for pollutants in the Greater Cape Town area, South Africa. White circles are capture locations of caracal individuals that were trapped and collared with GPS tracking devices. Black circles are opportunistically sampled individuals with buffers calculated around collection location that were mostly killed in vehicle accidents. Coloured areas on the map correspond to different land uses. The green line denotes the Table Mountain National Park (TMNP) boundary.

Fig. 4.2 Relationship between logged concentration of ΣPCB and ΣDDT in adipose and whole blood of caracals from the Greater Cape Town area, South Africa. All relationships were highly significant ($p < 0.001$).

Fig. 4.3 Parameter estimates and 95% confidence intervals for spatial variable LMMs of caracal blood (red) and adipose (orange) for concentrations of organochlorines in terms of wet (circle) and lipid (triangle) weight. Estimates are shown for those parameters included in the top models (as determined by AICc) including different land uses, human population density and electrical transformer density in the Greater Cape Town area.

Fig. 4.4 Organochlorine exposure risk maps for the Greater Cape Town area showing probability of exposure categorised into five risk levels based on spatial variable LMMs which contained continuous variables: (A) ΣDDT (based on the top blood l.w. model which included wetlands, vineyards, and human population density) and (B) ΣPCB (based on the top adipose l.w. model which included informal settlements and electrical transformer density).

Fig. 4.5 Relationship between blood organochlorine concentrations (log-transformed) and percentage diet (biomass) of (A) reptile, (B) insectivore, (C) carnivore and (D) exotic prey for caracals around Cape Town, South Africa.

Fig. 4.6 Parameter estimates and 95% confidence intervals for linear models of diet proportion (prey functional groups) and concentrations of organochlorines in caracal blood in terms of wet (circle) and lipid (triangle) weight. Estimates are shown for those parameters included in the top models (as determined by AICc).

Fig. 4.7 Parameter estimates and 95% confidence intervals for linear models of blood cell count and concentrations of organochlorines in caracal blood in terms of wet (circle) and lipid (triangle) weight. Estimates are shown for those parameters included in the top models (as determined by AICc).

Fig. 4.8 Parameter estimates and 95% confidence intervals for linear models of serum biochemistry and concentrations of organochlorines in caracal blood in terms of wet (circle) and lipid (triangle) weight. Estimates are shown for those parameters included in the top models (as determined by AICc).

Fig. 5.2 Maps of the urban-dominated, northern region of the Cape Peninsula showing (**A**) Table Mountain National Park (TMNP, in green); relevant spatial variables including (**B**) informal settlements, vineyards, wetlands and human population density (30 m^2) and (**C**) electrical transformer density (100 m^2); selection surfaces for (**D**) the most highly selected foraging areas (corresponding to selection levels 7-10 as presented in Chapter 3, Fig. 3.1); and heatmaps for probability of exposure to (**E**) sum of DDTs and (**F**) sum of PCBs (as presented in Chapter 4, Fig. 4.4).

Fig. 5.2 Untagged juvenile caracal hides behind restios (endemic reed-like plants). Cape Town's caracal rely on vegetative cover to reduce human detection risk and cover is more selected closer to the urban edge where perceived risk is potentially higher. Photograph by C. Meyer, Cape Town (2020).

Fig. 5.3 Photographs of TMC33 Hermes, an adult male caracal who was hit by a car in 2018 but tagged and released (see http://www.urbancaracal.org/meet-the-cats), that show his remarkable habituation to people and human structures. TMC33 is frequently sighted within Table Mountain National Park by tourists, hikers, mountain bikers and trail runners. Photographs by (A) G. Myata in 2019, (B) F. Sacks in 2020, (C) Y. Tromp in 2019 and (D) M. Pan in 2019.

Fig. 5.4 Cape Town's human landscapes as an ecotoxicological trap. Green areas are attractive to caracals for foraging (the urban edge, vineyards, and wetlands). Green dashed lines indicate selection for the urban edge. Red areas are identified potential sources of environmental pollutants (household/informal settlement use of pesticides and PCB-containing products, leakage from electrical equipment and agricultural use of pesticides, particularly in vineyards). Red dotted lines indicate likely pathways of exposure for caracals and their prey.

Fig. 5.5 Untagged juvenile caracal sitting on the road near a stop sign in Cape Point nature reserve in the southern Peninsula. The greatest cause of mortality for Cape Peninsula caracals is vehicle collisions. Photograph by L. Nelson (2020).

LIST OF ABBREVIATIONS

AIC	Akaike's Information Criterion
AICc	AIC corrected for small sample sizes
ANOVA	Analysis of Variance
ArcGIS	Aeronautical Reconnaissance Coverage GIS
CFO	Corrected Frequency of Occurrence
CFR	Cape Floristic Region
CI	Confidence Interval
CoCT	City of Cape Town Government
DDT	Dichloro-diphenyl-trichloroethane
DOI	Digital Object Identifier
EN	Endangered
ESKOM	Electricity Supply Commission of South Africa
ESRI	Environmental Systems Research Institute
g	Gram
GC-ECD	Gas Chromatography with an Electron Capture Detector
GIS	Geographic Information System
GPS	Global Positioning System
HCB	Hexachlorobenzene
HCH	Hexachlorocyclohexane
HR	Home Range
IUCN	International Union for Conservation of Nature
kg	Kilogram
km	Kilometres
KZN	KwaZulu-Natal Province
LC	Least Concern
LoCoH	Local Convex Hull
LOD	Limit of Detection
m	Metres
max	Maximum
min	Minimum
mL	Millilitre
n	Sample size
NBR2	Normalised Burn Ratio 2
NDVI	Normalised Difference Vegetation Index
NP	National Park
NT	Near Threatened
OC	Organochlorine
PA	Protected area
PBDE	Polybrominated diphenyl ether
PCB	Polychlorinated biphenyl
PLE	Pressurised Liquid Extraction
POP	Persistent Organic Pollutant
QGIS	Quantum GIS
RO	Relative Occurrence
SANParks	South African National Parks
SD	Standard Deviation
SE	Standard Error
TMNP	Table Mountain National Park
UCP	Urban Caracal Project
UCT	University of Cape Town
UNEP	United Nations Environment Programme
UNESCO	United Nations Educational, Scientific and Cultural Organization
USA	United States of America
VIF	Variance Inflation Factor
VU	Vulnerable
WC	Western Cape Province
WWF	World Wide Fund for Nature
µL	Microlitre

APPENDIX A

Materials for Chapter 2:

Appendix 2.1 Caracal prey on the Cape Peninsula, South Africa as determined by scat (*scat*) and unconsumed prey remains found at GPS clusters and opportunistically (*kill*). Kill biomass consumed was determined using percentages scaled to equivalent prey mass categories (Funston et al. 1998) and scat prey biomass consumed was estimated using a generalised felid biomass model Chakrabarti et al. (2016). Mean prey masses were determined by multiplying mean adult female weights (Skinner & Chimimba 2005, Hockey et al. 2005) by 0.75 (see *Methods in Chapter 2*).

Prey item		Count of prey items		Relative occurrence (RO)		Corrected frequency of occurrence (CFO)		Biomass consumed (kg)		% Biomass consumed	
Common name	Scientific name	kill	scat	kill	scat	kill	scat	kill	scat	kill	scat
Amphibian	**Amphibia**	**0**	**2**	**0.00**	**0.22**	**0.00**	**2.00**	**0.00**	**0.19**	**0.00**	**0.21**
Frog	**Anura**	**0**	**2**	**0.00**	**0.22**	**0.00**	**2.00**	**0.00**	**0.19**	**0.00**	**0.21**
Unknown	Unknown	0	2	0.00	0.22	0.00	2.00	0.00	0.19	0.00	0.21
Bird	**Aves**	**308**	**286**	**80.00**	**31.33**	**308.00**	**219.74**	**184.37**	**35.63**	**41.86**	**39.17**
Columbiform	**Columbiformes**	**51**	**8**	**13.25**	**0.88**	**51.00**	**5.41**	**7.86**	**0.58**	**1.79**	**0.64**
Cape turtle dove	*Streptopelia capicola*	6	0	1.56	0.00	6.00	0.00	0.61	0.00	0.14	0.00
Laughing dove	*Streptopelia senegalensis*	7	0	1.82	0.00	7.00	0.00	0.47	0.00	0.11	0.00
Red eyed dove	*Streptopelia semitorquata*	10	1	2.60	0.11	10.00	0.24	1.69	0.02	0.38	0.03
Rock dove	*Columba livia*	14	3	3.64	0.33	14.00	2.40	2.81	0.26	0.64	0.29
Speckled pigeon	*Columba guinea*	5	0	1.30	0.00	5.00	0.00	0.88	0.00	0.20	0.00
Unknown	Unknown	9	4	2.34	0.44	9.00	2.77	1.40	0.29	0.32	0.32
Galliform	**Galliformes**	**78**	**30**	**20.26**	**3.29**	**78.00**	**22.10**	**57.22**	**3.68**	**12.99**	**4.04**
Cape francolin	*Pternistis capensis*	8	3	2.08	0.33	8.00	1.15	2.08	0.14	0.47	0.15
Domestic chicken	*Gallus gallus domesticus*	1	0	0.26	0.00	1.00	0.00	1.48	0.00	0.34	0.00
Domestic peacock	*Pavo cristatus*	2	0	0.52	0.00	2.00	0.00	3.15	0.00	0.72	0.00
Grey-winged francolin	*Scleroptila africanus*	0	1	0.00	0.11	0.00	1.00	0.00	0.11	0.00	0.12
Guinea fowl	*Numida melaegris*	67	24	17.40	2.63	67.00	19.10	50.50	3.33	11.47	3.67
Unknown	Unknown	0	2	0.00	0.22	0.00	0.85	0.00	0.10	0.00	0.11
Pelecaniform	**Pelecaniformes**	**29**	**9**	**7.53**	**0.99**	**29.00**	**7.33**	**16.01**	**0.98**	**3.64**	**1.08**
African sacred ibis	*Threskiornis aethiopicus*	12	2	3.12	0.22	12.00	2.00	7.54	0.32	1.71	0.36
Black headed heron	*Ardea melanocephala*	1	0	0.26	0.00	1.00	0.00	0.36	0.00	0.08	0.00
Cattle egret	*Bubulcus ibis*	3	0	0.78	0.00	3.00	0.00	0.69	0.00	0.16	0.00
Hadeda ibis	*Bostrychia hagedash*	11	2	2.86	0.22	11.00	1.18	6.91	0.19	1.57	0.21
Little egret	*Egretta garzetta*	2	0	0.52	0.00	2.00	0.00	0.52	0.00	0.12	0.00
Unknown	Unknown	0	5	0.00	0.55	0.00	4.15	0.00	0.47	0.00	0.51
Raptors	**Accipitriformes & Strigiformes**	**3**	**1**	**0.78**	**0.11**	**3.00**	**0.15**	**1.18**	**0.02**	**0.27**	**0.02**
Jackal buzzard	*Buteo rufofuscus*	1	0	0.26	0.00	1.00	0.00	0.67	0.00	0.15	0.00
Rock kestrel	*Falco rupicolus*	1	0	0.26	0.00	1.00	0.00	0.16	0.00	0.04	0.00
Spotted eagle owl	*Bubo africanus*	1	1	0.26	0.11	1.00	0.15	0.35	0.02	0.08	0.02

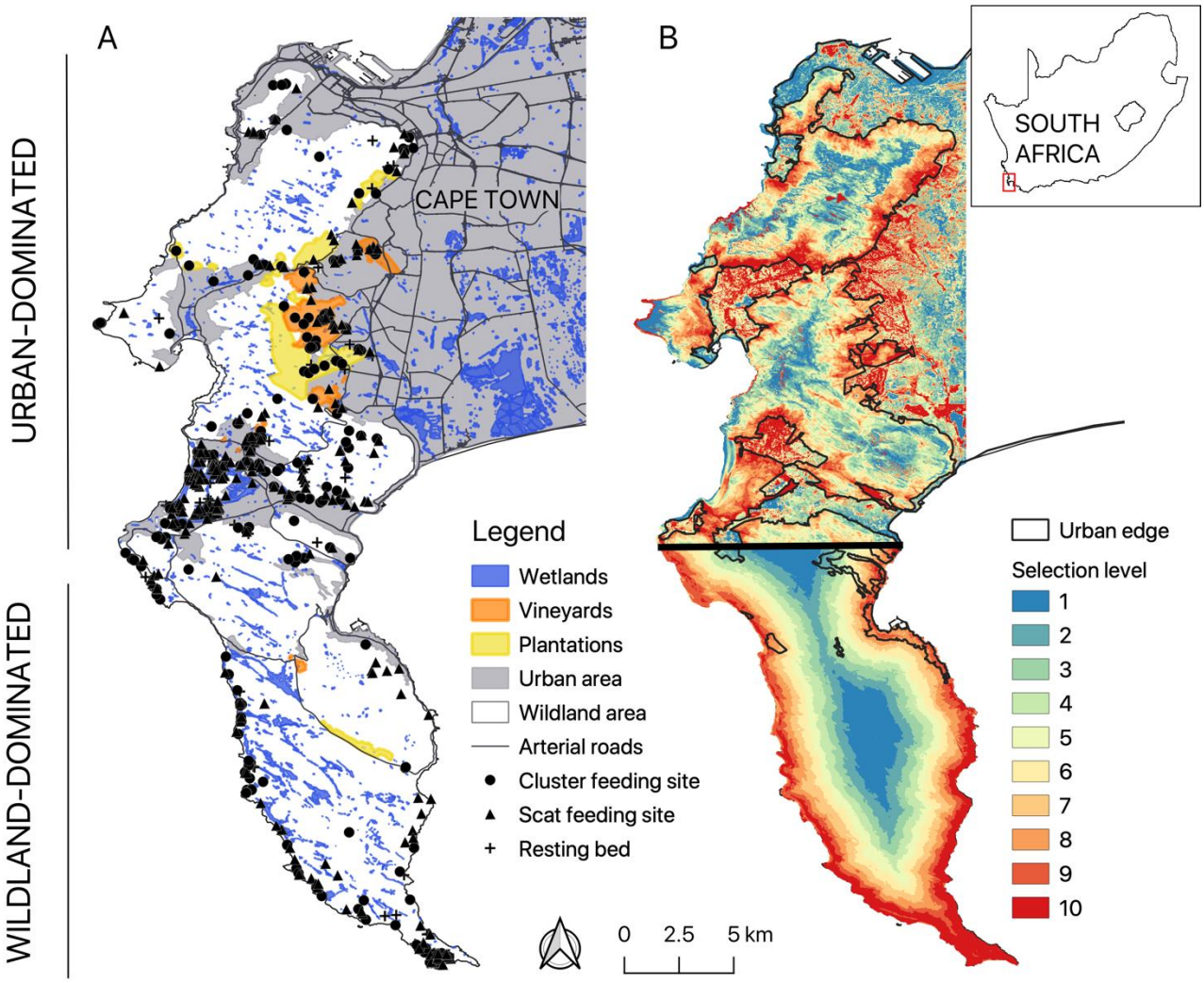
Prey item		Count of prey items		Relative occurrence (RO)		Corrected frequency of occurrence (CFO)		Biomass consumed (kg)		% Biomass consumed	
Common name	Scientific name	kill	scat	kill	scat	kill	scat	kill	scat	kill	scat
Seabirds & Shorebirds	**Charadriiformes, Sphenisciformes & Suliformes**	**78**	**130**	**20.26**	**14.24**	**78.00**	**107.18**	**52.58**	**17.70**	**11.94**	**19.46**
African black oystercatcher	*Haematopus moquini*	2	0	0.52	0.00	2.00	0.00	0.73	0.00	0.17	0.00
African penguin	*Spheniscus demersus*	11	21	2.86	2.30	11.00	17.74	16.03	4.08	3.64	4.49
Bank cormorant	*Phalacrocorax neglectus*	0	1	0.00	0.11	0.00	0.13	0.00	0.02	0.00	0.03
Cape cormorant	*Phalacrocorax capensis*	42	90	10.91	9.86	42.00	73.48	23.22	11.28	5.27	12.40
Cape gannet	*Morus capensis*	1	0	0.26	0.00	1.00	0.00	1.31	0.00	0.30	0.00
Common tern	*Sterna hirundo*	0	2	0.00	0.22	0.00	2.00	0.00	0.17	0.00	0.19
Crowned cormorant	*Phalacrocorax coronatus*	0	4	0.00	0.44	0.00	3.08	0.00	0.40	0.00	0.44
Hartlaubs gull	*Larus hartlaubii*	2	1	0.52	0.11	2.00	1.00	0.36	0.10	0.08	0.11
Kelp gull	*Larus dominicanus*	10	3	2.60	0.33	10.00	2.98	4.12	0.41	0.94	0.45
Sandwich tern	*Sterna sandvicensis*	1	0	0.26	0.00	1.00	0.00	0.18	0.00	0.04	0.00
Swift tern	*Sterna bergii*	1	0	0.26	0.00	1.00	0.00	0.19	0.00	0.04	0.00
White-breasted cormorant	*Phalacrocorax lucidus*	6	6	1.56	0.66	6.00	5.70	6.03	1.13	1.37	1.24
Unknown	Unknown	2	2	0.52	0.22	2.00	1.08	0.42	0.10	0.10	0.11
Passerines & Cuckoos	**Passeriformes & Cuculiformes**	**8**	**6**	**2.08**	**0.66**	**8.00**	**3.95**	**0.79**	**0.37**	**0.18**	**0.41**
Cape bulbul	*Pycnonotus capensis*	1	0	0.26	0.00	1.00	0.00	0.03	0.00	0.01	0.00
Olive thrush	*Turdus olivaceus*	3	0	0.78	0.00	3.00	0.00	0.15	0.00	0.03	0.00
Pied crow	*Corvus albus*	1	0	0.26	0.00	1.00	0.00	0.28	0.00	0.06	0.00
Red-winged starling	*Onychognathus morio*	1	0	0.26	0.00	1.00	0.00	0.09	0.00	0.02	0.00
Burchell's coucal	*Centropus burchellii*	1	0	0.26	0.00	1.00	0.00	0.12	0.00	0.03	0.00
Unknown	Unknown	1	6	0.26	0.66	1.00	3.95	0.13	0.37	0.03	0.41
Waterbird	**Anseriformes**	**57**	**66**	**14.81**	**7.23**	**57.00**	**47.56**	**46.51**	**8.30**	**10.56**	**9.12**
Cape teal	*Anas capensis*	1	1	0.26	0.11	1.00	0.24	0.19	0.03	0.04	0.03
Domestic goose	*Anser anser*	2	0	0.52	0.00	2.00	0.00	1.88	0.00	0.43	0.00
Egyptian goose	*Alopochen aegyptiaca*	36	39	9.35	4.27	36.00	30.80	33.83	5.91	7.68	6.49
Mallard	*Anas platyrhynchos*	4	0	1.04	0.00	4.00	0.00	2.01	0.00	0.46	0.00
Spurwinged goose	*Plectropterus gambensis*	1	1	0.26	0.11	1.00	0.65	1.58	0.16	0.36	0.18
Yellow-billed duck	*Anas undulata*	7	12	1.82	1.31	7.00	7.37	2.88	1.01	0.65	1.11
Unknown	Unknown	6	13	1.56	1.42	6.00	8.51	4.14	1.19	0.94	1.31
Unknown bird	**Unknown**	**4**	**36**	**1.04**	**3.94**	**4.00**	**26.06**	**2.22**	**4.00**	**0.50**	**4.40**
Insect	**Insecta**	**0**	**13**	**0.00**	**1.42**	**0.00**	**6.00**	**0.00**	**0.48**	**0.00**	**0.52**
Beetle	**Coleoptera**	**0**	**3**	**0.00**	**0.33**	**0.00**	**0.80**	**0.00**	**0.06**	**0.00**	**0.07**
Unknown insect	**Unknown**	**0**	**10**	**0.00**	**1.10**	**0.00**	**5.20**	**0.00**	**0.41**	**0.00**	**0.45**
Mammal	**Mammalia**	**76**	**575**	**19.74**	**62.98**	**76.00**	**371.20**	**255.73**	**51.75**	**58.06**	**56.89**
Bovid	**Bovidae**	**17**	**16**	**4.42**	**1.75**	**17.00**	**13.46**	**188.51**	**4.29**	**42.80**	**4.71**
Bontebok	*Damaliscus pygargus*	4	0	1.04	0.00	4.00	0.00	107.28	0.00	24.36	0.00

Prey item		Count of prey items		Relative occurrence (RO)		Corrected frequency of occurrence (CFO)		Biomass consumed (kg)		% Biomass consumed	
Common name	Scientific name	kill	scat	kill	scat	kill	scat	kill	scat	kill	scat
Domestic goat	*Capra aegagrus hircus*	1	0	0.26	0.00	1.00	0.00	9.00	0.00	2.04	0.00
Domestic sheep	*Ovis aries*	1	0	0.26	0.00	1.00	0.00	20.25	0.00	4.60	0.00
Grysbok	*Raphicerus melanotis*	11	16	2.86	1.75	11.00	13.46	51.98	4.29	11.80	4.71
Carnivore	**Carnivora**	**24**	**46**	**6.23**	**5.04**	**24.00**	**30.88**	**32.15**	**6.11**	**7.30**	**6.71**
Cape grey mongoose	*Galerella pulverulenta*	3	16	0.78	1.75	3.00	9.26	1.05	1.20	0.24	1.31
Domestic cat	*Felis catus*	17	12	4.42	1.31	17.00	9.99	27.54	2.50	6.25	2.74
Domestic dog	*Canis lupus familiaris*	0	1	0.00	0.11	0.00	0.01	0.00	0.00	0.00	0.00
Large spotted genet	*Genetta tigrina*	4	6	1.04	0.66	4.00	3.74	3.56	0.70	0.81	0.77
Mongoose	*Galerella sp.*	0	3	0.00	0.33	0.00	1.50	0.00	0.27	0.00	0.30
Water mongoose	*Atilax paludinosus*	0	7	0.00	0.77	0.00	5.39	0.00	1.19	0.00	1.31
Unknown	Unknown	0	1	0.00	0.11	0.00	1.00	0.00	0.25	0.00	0.28
Medium mammal	**Hyracoidea & Incognita**	**14**	**81**	**3.64**	**8.87**	**14.00**	**71.45**	**22.93**	**16.60**	**5.21**	**18.25**
Rock hyrax	*Procavia capensis*	14	69	3.64	7.56	14.00	59.65	22.93	14.36	5.21	15.79
Unknown	Unknown	0	12	0.00	1.31	0.00	11.80	0.00	2.24	0.00	2.46
Rodent	**Rodentia**	**17**	**381**	**4.42**	**41.73**	**17.00**	**227.94**	**9.45**	**21.53**	**2.15**	**23.67**
African marsh rat	*Dasymys incontus*	0	1	0.00	0.11	0.00	0.70	0.00	0.06	0.00	0.07
African porcupine	*Hystrix africaeustralis*	1	1	0.26	0.11	1.00	1.00	6.17	0.32	1.40	0.36
African pygmy mouse	*Mus minutoides*	0	13	0.00	1.42	0.00	1.58	0.00	0.13	0.00	0.14
Brown rat	*Rattus norvegicus*	0	8	0.00	0.88	0.00	6.13	0.00	0.60	0.00	0.66
Cape dune mole-rat	*Bathyergus suillus*	4	15	1.04	1.64	4.00	12.03	1.35	1.53	0.31	1.69
Cape gerbil	*Gerbilliscus afra*	0	8	0.00	0.88	0.00	4.11	0.00	0.35	0.00	0.39
Cape mole-rat	*Georhychus capensis*	0	4	0.00	0.44	0.00	2.96	0.00	0.28	0.00	0.30
Four-striped grass mouse	*Rhabdomys pumilio*	0	62	0.00	6.79	0.00	38.55	0.00	3.16	0.00	3.48
Grey climbing mouse	*Dendromus melanotis*	0	6	0.00	0.66	0.00	1.34	0.00	0.11	0.00	0.12
Grey squirrel	*Sciurus carolinensis*	7	40	1.82	4.38	7.00	28.61	1.41	3.13	0.32	3.44
Namaqua rock rat	*Micaelamys namaquensis*	0	4	0.00	0.44	0.00	1.68	0.00	0.14	0.00	0.15
Saunder's vlei rat	*Otomys saundersiae*	0	11	0.00	1.20	0.00	6.21	0.00	0.54	0.00	0.59
Southern African vlei rat	*Otomys irroratus*	1	166	0.26	18.18	1.00	97.45	0.10	8.90	0.02	9.78
Verreaux's mouse	*Myomyscus verreauxii*	0	2	0.00	0.22	0.00	1.30	0.00	0.11	0.00	0.12
Vlei rat	*Otomys sp.*	1	26	0.26	2.85	1.00	15.34	0.10	1.36	0.02	1.50
Unknown	Unknown	3	14	0.78	1.53	3.00	8.97	0.33	0.81	0.07	0.89
Small mammal	**Soricidae & Chrysochloridae**	**3**	**44**	**0.78**	**4.82**	**3.00**	**22.64**	**0.05**	**1.83**	**0.01**	**2.01**
Cape golden mole	*Chrysochloris asiatica*	1	9	0.26	0.99	1.00	5.52	0.02	0.45	0.00	0.49
Reddish-grey musk shrew	*Crocidura cyanea*	0	19	0.00	2.08	0.00	7.98	0.00	0.64	0.00	0.70
Greater red musk shrew	*Crocidura flavescens*	0	7	0.00	0.77	0.00	3.03	0.00	0.25	0.00	0.27
Lesser dwarf shrew	*Suncus varilla*	0	2	0.00	0.22	0.00	0.47	0.00	0.04	0.00	0.04

Prey item		Count of prey items		Relative occurrence (RO)		Corrected frequency of occurrence (CFO)		Biomass consumed (kg)		% Biomass consumed	
Common name	Scientific name	kill	scat	kill	scat	kill	scat	kill	scat	kill	scat
Unknown	Unknown	2	7	0.52	0.77	2.00	5.65	0.03	0.46	0.01	0.50
Unknown mammal	**Unknown**	**1**	**7**	**0.26**	**0.77**	**1.00**	**4.83**	**2.64**	**1.40**	**0.60**	**1.54**
Reptile	**Reptilia**	**1**	**37**	**0.26**	**4.05**	**1.00**	**15.07**	**0.33**	**2.92**	**0.08**	**3.21**
Squamate	**Squamata**	**1**	**34**	**0.26**	**3.72**	**1.00**	**13.81**	**0.33**	**2.70**	**0.08**	**2.96**
Black girdled lizard	*Cordylus niger*	1	0	0.26	0.00	1.00	0.00	0.33	0.00	0.08	0.00
Common puff adder	*Bitis arietans*	0	3	0.00	0.33	0.00	2.75	0.00	0.66	0.00	0.72
Mole snake	*Pseudaspis cana*	0	10	0.00	1.10	0.00	5.00	0.00	0.99	0.00	1.08
Unknown	Unknown	0	21	0.00	2.30	0.00	6.07	0.00	1.05	0.00	1.16
Unknown reptile	**Unknown**	**0**	**3**	**0.00**	**0.33**	**0.00**	**1.26**	**0.00**	**0.22**	**0.00**	**0.25**
Grand Total		385	913			385.00	614.00	440.43	90.96		

APPENDIX B

Materials for Chapter 3:



Appendix 3.1 Cape Peninsula study area showing (**A**) feeding clusters (circles, n = 326), back-traced scats feeding events (triangles, n = 384) and resting beds (crosses, n = 117), and (**B**) selection surface for urban-dominated and wildland-dominated regions with estimates based on the top COVER integrated-diet (scaled) RSF models. Higher values indicate stronger positive selection.

Appendix 3.2 Top model results for LAND-USE/AGE/SEX based on AICc for resting beds and each foraging dataset (prey remains found at GPS clusters, scats, and integrated-diet) and digestion time (minimum, maximum and scaled to prey biomass) for caracals in urban- and wildland-dominated regions of the Cape Peninsula, South Africa.

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
Urban-dominated	Feeding clusters	Distance to urban edge	urban_edge_dist	-2.49	0.71	-3.53	0.000417151
		Distance to wetland	wetlands_dist	-0.17	0.10	-1.76	0.078834625
		NDVI	ndvi	0.80	0.10	8.12	4.64E-16
		Slope	slope	-0.57	0.14	-4.06	4.96E-05
		Age	adult	-5.77	2.78	-2.08	0.037543593
			juvenile	-27.69	3.18	-8.72	2.80E-18
		Landuse	plantations	-0.75	0.46	-1.61	0.107449776
			vines	0.55	0.40	1.36	0.17247101
			altered_open	-0.40	0.39	-1.02	0.305822149
			urban	-0.68	0.22	-3.12	0.001808492
	Scat: scaled	Distance to urban edge	urban_edge_dist	-1.26	0.52	-2.40	0.016224249
		Distance to wetland	wetlands_dist	-0.32	0.09	-3.50	0.000472274
		NDVI	ndvi	0.59	0.09	6.81	9.64E-12
		Slope	slope	-0.53	0.13	-4.15	3.35E-05
		Age	adult	-5.05	2.74	-1.84	0.065572478
			juvenile	-26.59	3.25	-8.19	2.54E-16
		Landuse	plantations	-1.12	0.52	-2.17	0.029633794
			vines	0.20	0.38	0.52	0.603389963
			altered_open	0.13	0.38	0.34	0.733626502
			urban	-0.50	0.19	-2.59	0.009618233
	Scat: min	Distance to urban edge	urban_edge_dist	-1.36	0.53	-2.55	0.010619502
		Distance to wetland	wetlands_dist	-0.35	0.09	-3.66	0.000253561
		NDVI	ndvi	0.58	0.08	6.84	7.88E-12
		Slope	slope	-0.56	0.13	-4.32	1.59E-05
		Age	adult	-5.05	2.74	-1.84	0.065907722
			juvenile	-26.69	3.24	-8.23	1.92E-16
		Landuse	plantations	-0.96	0.52	-1.83	0.067702443

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
			vines	0.57	0.38	1.49	0.136560647
			altered_open	0.17	0.37	0.46	0.645070914
			urban	-0.43	0.19	-2.25	0.024514533
	Scat: max	Distance to urban edge	urban_edge_dist	-1.27	0.53	-2.40	0.016565962
		Distance to wetland	wetlands_dist	-0.33	0.09	-3.52	0.000432987
		NDVI	ndvi	0.63	0.09	7.11	1.14E-12
		Slope	slope	-0.59	0.13	-4.54	5.55E-06
		Age	adult	-5.04	2.76	-1.83	0.067651195
			juvenile	-26.74	3.26	-8.21	2.18E-16
		Landuse	plantations	-0.88	0.52	-1.69	0.090166766
			vines	0.28	0.38	0.72	0.469943119
			altered_open	0.01	0.38	0.03	0.978020476
			urban	-0.43	0.19	-2.22	0.02658689
	Integrated: scaled	Distance to urban edge	urban_edge_dist	-1.89	0.41	-4.59	4.45E-06
		Distance to wetland	wetlands_dist	-0.26	0.07	-3.91	9.12E-05
		NDVI	ndvi	0.52	0.06	8.24	1.72E-16
		Slope	slope	-0.43	0.09	-4.90	9.44E-07
		Landuse	natural	-4.75	2.94	-1.62	0.106029244
			plantations	-5.57	2.96	-1.88	0.059985061
			vines	-4.38	2.96	-1.48	0.138279864
			altered_open	-4.75	2.96	-1.61	0.107799637
			urban	-5.29	2.95	-1.80	0.072480397
		Age	juvenile	-23.26	2.90	-8.02	1.09E-15
	Integrated: min	Distance to urban edge	urban_edge_dist	-2.07	0.43	-4.87	1.10E-06
		Distance to wetland	wetlands_dist	-0.24	0.07	-3.57	0.000362852
		NDVI	ndvi	0.71	0.07	10.90	1.13E-27
		Slope	slope	-0.57	0.10	-5.75	8.69E-09
		Age	adult	-4.84	2.98	-1.63	0.103720366
			juvenile	-28.42	3.42	-8.31	9.68E-17

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
		Landuse	plantations	-0.87	0.35	-2.51	0.012043409
			vines	0.37	0.27	1.35	0.177136252
			altered_open	-0.09	0.27	-0.34	0.730633815
			urban	-0.60	0.14	-4.13	3.56E-05
	Integrated: max	Distance to urban edge	urban_edge_dist	-1.34	0.40	-3.33	0.000869925
		Distance to wetland	wetlands_dist	-0.29	0.07	-4.34	1.43E-05
		NDVI	ndvi	0.65	0.06	10.06	7.90E-24
		Slope	slope	-0.36	0.09	-4.18	2.92E-05
		Age	adult	-4.67	2.92	-1.60	0.110376249
			juvenile	-27.80	3.34	-8.32	8.72E-17
		Landuse	plantations	-0.81	0.37	-2.20	0.02795331
			vines	0.35	0.29	1.23	0.21716927
			altered_open	-0.16	0.30	-0.53	0.596278405
			urban	-0.33	0.14	-2.34	0.019378536
Wildland-dominated	Feeding clusters	Distance to urban edge	urban_edge_dist	0.16	0.09	1.79	0.07276807
		Distance to coast	coast_dist	-7.08	0.92	-7.66	1.84E-14
		NDVI	ndvi	0.67	0.13	4.99	6.05E-07
		Slope	slope	-0.30	0.16	-1.86	0.062384947
		Sex	female	-19.50	1.11	-17.49	1.61E-68
			male	-18.84	1.12	-16.77	3.83E-63
	Scat: scaled	Distance to urban edge	urban_edge_dist	0.87	0.13	6.77	1.25E-11
		Distance to coast	coast_dist	-4.04	0.72	-5.59	2.24E-08
		Distance to wetland	wetlands_dist	0.32	0.11	3.00	0.002718248
		NDVI	ndvi	0.55	0.12	4.50	6.78E-06
		Slope	slope	-0.18	0.12	-1.47	0.140549659
		Sex	female	-17.63	0.84	-21.00	5.99E-98
			male	-17.67	0.85	-20.76	1.02E-95
	Scat: min	Distance to urban edge	urban_edge_dist	0.91	0.13	7.09	1.38E-12
		Distance to coast	coast_dist	-4.44	0.78	-5.72	1.07E-08

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
		Distance to wetland	wetlands_dist	0.18	0.10	1.82	0.0693924
		NDVI	ndvi	0.43	0.13	3.26	0.001101591
		Sex	female	-18.12	0.91	-19.91	3.31E-88
			male	-18.10	0.91	-19.86	9.41E-88
	Scat: max	Distance to urban edge	urban_edge_dist	0.87	0.13	6.94	3.87E-12
		Distance to coast	coast_dist	-4.12	0.71	-5.76	8.32E-09
		Distance to wetland	wetlands_dist	0.29	0.10	3.01	0.002603623
		Slope	slope	-0.18	0.14	-1.34	0.180398406
		NDVI	ndvi	0.45	0.13	3.35	0.00081666
		Sex	female	-17.72	0.82	-21.58	2.54E-103
			male	-17.54	0.83	-21.16	2.25E-99
	Integrated: scaled	Distance to urban edge	urban_edge_dist	0.27	0.06	4.54	5.53E-06
		Distance to coast	coast_dist	-4.62	0.47	-9.74	2.11E-22
		NDVI	ndvi	0.43	0.09	4.63	3.66E-06
		Slope	slope	0.15	0.07	2.26	0.023659701
		Sex	female	-16.75	0.55	-30.36	1.87E-202
			male	-16.31	0.54	-30.05	2.32E-198
	Integrated: min	Distance to urban edge	urban_edge_dist	0.51	0.08	6.75	1.47E-11
		Distance to coast	coast_dist	-6.17	0.60	-10.28	9.07E-25
		NDVI	ndvi	0.55	0.09	6.08	1.21E-09
		Slope	slope	-0.20	0.09	-2.18	0.029428432
		Sex	female	-19.46	0.82	-23.69	4.72E-124
			male	-18.52	0.80	-23.16	1.07E-118
	Integrated: max	Distance to urban edge	urban_edge_dist	0.38	0.07	5.83	5.68E-09
		Distance to coast	coast_dist	-4.44	0.46	-9.67	3.87E-22
		NDVI	ndvi	0.37	0.08	4.58	4.74E-06
		Sex	female	-16.74	0.53	-31.62	1.79E-219
			male	-16.36	0.53	-30.92	6.05E-210

Appendix 3.3 Top model results for LAND-USE/SEX based on AICc for resting beds and each foraging dataset (prey remains found at GPS clusters, scats, and integrated-diet) and digestion time (minimum, maximum and scaled to prey biomass) for caracals in urban- and wildland-dominated regions of the Cape Peninsula, South Africa.

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
Urban-dominated	Feeding clusters	Distance to urban edge	urban_edge_dist	-2.35	0.65	-3.65	0.000262875
		Distance to coast	coast_dist	-0.23	0.07	-3.33	0.000877159
		NDVI	ndvi	0.82	0.08	9.90	3.97E-23
		Slope	slope	-0.47	0.10	-4.65	3.33E-06
		Landuse	natural	-12.85	0.31	-41.70	0
			plantations	-13.25	0.45	-29.28	1.75E-188
			vines	-12.10	0.45	-26.74	1.44E-157
			altered_open	-12.96	0.49	-26.20	2.60E-151
			urban	-13.48	0.40	-33.72	3.18E-249
	Scat: scaled	Distance to urban edge	urban_edge_dist	-1.53	0.49	-3.11	0.001841676
		Distance to wetland	wetlands_dist	-0.22	0.08	-2.78	0.005412744
		NDVI	ndvi	0.52	0.07	7.05	1.77E-12
		Slope	slope	-0.24	0.09	-2.62	0.008879351
		Landuse	natural	-12.22	0.20	-59.86	0
			plantations	-13.35	0.50	-26.62	4.48E-156
			vines	-12.14	0.38	-31.88	5.28E-223
			altered_open	-11.95	0.43	-27.98	3.07E-172
			urban	-12.79	0.30	-42.80	0
	Scat: min	Distance to urban edge	urban_edge_dist	-1.43	0.49	-2.89	0.003858155
		Distance to wetland	wetlands_dist	-0.24	0.08	-2.98	0.002850693
		NDVI	ndvi	0.51	0.07	6.98	3.04E-12
		Slope	slope	-0.23	0.09	-2.54	0.011012378
		Landuse	natural	-12.20	0.21	-58.77	0
			plantations	-13.26	0.50	-26.41	9.34E-154
			vines	-11.85	0.38	-31.05	1.21E-211
			altered_open	-11.99	0.42	-28.25	1.56E-175
			urban	-12.71	0.30	-42.15	0

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
	Scat: max	Distance to urban edge	urban_edge_dist	-1.40	0.49	-2.83	0.004641566
		Distance to wetland	wetlands_dist	-0.21	0.08	-2.65	0.008102679
		NDVI	ndvi	0.54	0.08	7.15	8.67E-13
		Slope	slope	-0.25	0.09	-2.80	0.005176252
		Landuse	natural	-12.20	0.21	-59.08	0
			plantations	-13.25	0.50	-26.34	7.01E-153
			vines	-12.07	0.38	-31.49	1.32E-217
			altered_open	-12.05	0.43	-28.10	8.68E-174
			urban	-12.67	0.30	-42.01	0
	Integrated: scaled	Distance to urban edge	urban_edge_dist	-1.72	0.38	-4.50	6.77E-06
		Distance to wetland	wetlands_dist	-0.14	0.06	-2.59	0.009603322
		Distance to coast	coast_dist	-0.14	0.05	-2.90	0.003715754
		NDVI	ndvi	0.57	0.06	10.28	8.60E-25
		Slope	slope	-0.26	0.07	-3.44	0.000588553
		Landuse	natural	-12.36	0.17	-73.25	0
			plantations	-13.02	0.32	-41.23	0
			vines	-11.76	0.30	-39.15	0
			altered_open	-12.34	0.33	-37.89	0
			urban	-12.83	0.24	-54.55	0
	Integrated: min	Distance to urban edge	urban_edge_dist	-2.13	0.39	-5.42	6.07E-08
		Distance to wetland	wetlands_dist	-0.14	0.06	-2.54	0.011033591
		Distance to coast	coast_dist	-0.13	0.05	-2.64	0.008246284
		NDVI	ndvi	0.69	0.06	11.94	7.05E-33
		Slope	slope	-0.31	0.08	-3.88	0.000103991
		Landuse	natural	-12.58	0.18	-71.34	0
			plantations	-13.28	0.32	-41.19	0
			vines	-12.14	0.29	-41.62	0
			altered_open	-12.72	0.33	-38.86	0
			urban	-13.19	0.24	-54.45	0

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
	Integrated: max	Distance to urban edge	urban_edge_dist	-1.20	0.37	-3.26	0.001127178
		Distance to wetland	wetlands_dist	-0.18	0.06	-3.27	0.001060382
		Distance to coast	coast_dist	-0.18	0.05	-3.81	0.000136381
		NDVI	ndvi	0.71	0.06	12.28	1.15E-34
		Slope	slope	-0.23	0.07	-3.22	0.001296355
		Landuse	natural	-12.21	0.16	-76.09	0
			plantations	-12.85	0.33	-38.71	0
			vines	-11.61	0.29	-40.43	0
			altered_open	-12.03	0.33	-36.91	2.96E-298
			urban	-12.49	0.23	-54.72	0
Wildland-dominated	Feeding clusters	Distance to urban edge	urban_edge_dist	0.16	0.09	1.79	0.07276807
		Distance to coast	coast_dist	-7.08	0.92	-7.66	1.84E-14
		NDVI	ndvi	0.67	0.13	4.99	6.05E-07
		Slope	slope	-0.30	0.16	-1.86	0.062384947
		Sex	female	-19.50	1.11	-17.49	1.61E-68
			male	-18.84	1.12	-16.77	3.83E-63
	Scat: scaled	Distance to urban edge	urban_edge_dist	0.87	0.13	6.77	1.25E-11
		Distance to coast	coast_dist	-4.04	0.72	-5.59	2.24E-08
		Distance to wetland	wetlands_dist	0.32	0.11	3.00	0.002718248
		NDVI	ndvi	0.55	0.12	4.50	6.78E-06
		Slope	slope	-0.18	0.12	-1.47	0.140549659
		Sex	female	-17.63	0.84	-21.00	5.99E-98
			male	-17.67	0.85	-20.76	1.02E-95
	Scat: min	Distance to urban edge	urban_edge_dist	0.91	0.13	7.09	1.38E-12
		Distance to coast	coast_dist	-4.44	0.78	-5.72	1.07E-08
		Distance to wetland	wetlands_dist	0.18	0.10	1.82	0.0693924
		NDVI	ndvi	0.43	0.13	3.26	0.001101591
		Sex	female	-18.12	0.91	-19.91	3.31E-88
			male	-18.10	0.91	-19.86	9.41E-88

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
	Scat: max	Distance to urban edge	urban_edge_dist	0.87	0.13	6.94	3.87E-12
		Distance to coast	coast_dist	-4.12	0.71	-5.76	8.32E-09
		Distance to wetland	wetlands_dist	0.29	0.10	3.01	0.002603623
		Slope	slope	-0.18	0.14	-1.34	0.180398406
		NDVI	ndvi	0.45	0.13	3.35	0.00081666
		Sex	female	-17.72	0.82	-21.58	2.54E-103
			male	-17.54	0.83	-21.16	2.25E-99
	Integrated: scaled	Distance to urban edge	urban_edge_dist	0.27	0.06	4.54	5.53E-06
		Distance to coast	coast_dist	-4.62	0.47	-9.74	2.11E-22
		NDVI	ndvi	0.43	0.09	4.63	3.66E-06
		Slope	slope	0.15	0.07	2.26	0.023659701
		Sex	female	-16.75	0.55	-30.36	1.87E-202
			male	-16.31	0.54	-30.05	2.32E-198
	Integrated: min	Distance to urban edge	urban_edge_dist	0.51	0.08	6.75	1.47E-11
		Distance to coast	coast_dist	-6.17	0.60	-10.28	9.07E-25
		NDVI	ndvi	0.55	0.09	6.08	1.21E-09
		Slope	slope	-0.20	0.09	-2.18	0.029428432
		Sex	female	-19.46	0.82	-23.69	4.72E-124
			male	-18.52	0.80	-23.16	1.07E-118
	Integrated: max	Distance to urban edge	urban_edge_dist	0.38	0.07	5.83	5.68E-09
		Distance to coast	coast_dist	-4.44	0.46	-9.67	3.87E-22
		NDVI	ndvi	0.37	0.08	4.58	4.74E-06
		Sex	female	-16.74	0.53	-31.62	1.79E-219
			male	-16.36	0.53	-30.92	6.05E-210

Appendix 3.4 Top model results for COVER/AGE/SEX based on AICc for resting beds and each foraging dataset (prey remains found at GPS clusters, scats, and integrated-diet) and digestion time (minimum, maximum and scaled to prey biomass) for caracals in urban- and wildland-dominated regions of the Cape Peninsula, South Africa.

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
Urban-dominated	Feeding clusters	Distance to urban edge	urban_edge_dist	-5.04	0.87	-5.82	5.79E-09
		Cover	high	-7.11	2.80	-2.54	0.011181153
			low	-1.44	2.80	-0.52	0.605736136
		Distance to wetland	wetlands_dist	-0.20	0.10	-2.08	0.037850348
		NDVI	ndvi	0.72	0.09	7.71	1.29E-14
		Slope	slope	-0.52	0.14	-3.84	0.000121701
		Age	juvenile	-21.94	2.79	-7.87	3.64E-15
		Cover*Distance to urban edge	urban_edge_dist:low	12.10	1.19	10.16	3.09E-24
	Scat: scaled	Distance to urban edge	urban_edge_dist	-2.11	0.56	-3.78	0.000159148
		Cover	high	-5.45	2.75	-1.98	0.047598017
			low	-2.42	2.77	-0.87	0.38197855
		Distance to wetland	wetlands_dist	-0.35	0.09	-3.84	0.000121192
		NDVI	ndvi	0.57	0.09	6.64	3.18E-11
		Slope	slope	-0.58	0.13	-4.46	8.22E-06
		Age	juvenile	-21.62	2.81	-7.71	1.30E-14
		Cover*Distance to urban edge	urban_edge_dist:low	7.66	0.99	7.71	1.27E-14
	Scat: min	Distance to urban edge	urban_edge_dist	-2.36	0.57	-4.14	3.49E-05
		Cover	high	-5.50	2.75	-2.00	0.045404031
			low	-2.78	2.76	-1.01	0.314505398
		Distance to wetland	wetlands_dist	-0.38	0.09	-4.16	3.24E-05
		NDVI	ndvi	0.55	0.09	6.36	2.02E-10
		Slope	slope	-0.60	0.13	-4.49	7.07E-06
		Age	juvenile	-21.66	2.80	-7.74	1.01E-14
		Cover*Distance to urban edge	urban_edge_dist:low	6.92	0.94	7.34	2.19E-13
	Scat: max	Distance to urban edge	urban_edge_dist	-2.32	0.57	-4.05	5.02E-05

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
		Cover	high	-5.48	2.76	-1.98	0.047513721
			low	-2.99	2.78	-1.08	0.281263698
		Distance to wetland	wetlands_dist	-0.38	0.09	-4.03	5.57E-05
		NDVI	ndvi	0.56	0.09	6.61	3.94E-11
		Slope	slope	-0.59	0.13	-4.50	6.89E-06
		Age	juvenile	-21.77	2.81	-7.74	9.67E-15
		Cover*Distance to urban edge	urban_edge_dist:low	6.51	0.91	7.13	1.01E-12
	Integrated: scaled	Distance to urban edge	urban_edge_dist	-3.10	0.46	-6.76	1.43E-11
		Cover	high	-5.33	2.95	-1.80	0.07120397
			low	-2.06	2.96	-0.69	0.487095222
		Distance to wetland	wetlands_dist	-0.29	0.07	-4.44	9.05E-06
		NDVI	ndvi	0.49	0.06	7.85	4.16E-15
		Slope	slope	-0.45	0.09	-5.06	4.25E-07
		Age	juvenile	-23.36	2.92	-8.00	1.25E-15
		Cover*Distance to urban edge	urban_edge_dist:low	7.81	0.70	11.23	3.05E-29
	Integrated: min	Distance to urban edge	urban_edge_dist	-3.45	0.48	-7.27	3.53E-13
		Cover	high	-5.54	2.99	-1.85	0.063828584
			low	-1.38	2.99	-0.46	0.644425669
		Distance to wetland	wetlands_dist	-0.30	0.07	-4.51	6.36E-06
		NDVI	ndvi	0.68	0.06	10.75	6.00E-27
		Slope	slope	-0.59	0.10	-6.11	1.01E-09
		Age	juvenile	-23.66	2.96	-8.00	1.29E-15
		Cover*Distance to urban edge	urban_edge_dist:low	9.47	0.71	13.37	8.97E-41
	Integrated: max	Distance to urban edge	urban_edge_dist	-1.92	0.43	-4.45	8.48E-06
		Cover	high	-5.04	2.93	-1.72	0.085200678
			low	-2.11	2.94	-0.72	0.472081495
		Distance to wetland	wetlands_dist	-0.32	0.06	-4.92	8.72E-07

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
		NDVI	ndvi	0.69	0.06	10.69	1.10E-26
		Slope	slope	-0.36	0.08	-4.31	1.66E-05
		Age	juvenile	-23.19	2.89	-8.02	1.10E-15
		Cover*Distance to urban edge	urban_edge_dist:low	5.71	0.67	8.56	1.14E-17
Wildland-dominated	Feeding clusters	Distance to urban edge	urban_edge_dist	0.16	0.09	1.79	0.07276807
		Distance to coast	coast_dist	-7.08	0.92	-7.66	1.84E-14
		NDVI	ndvi	0.67	0.13	4.99	6.05E-07
		Slope	slope	-0.30	0.16	-1.86	0.062384947
		Sex	female	-19.50	1.11	-17.49	1.61E-68
			male	-18.84	1.12	-16.77	3.83E-63
	Scat: scaled	Distance to urban edge	urban_edge_dist	1.15	0.16	6.98	2.90E-12
		Cover	high	-19.61	1.07	-18.34	3.70E-75
			low	-18.39	1.23	-14.90	3.13E-50
		Distance to coast	coast_dist	-5.21	0.90	-5.77	7.86E-09
		Distance to wetland	wetlands_dist	0.43	0.11	3.81	0.000137348
		Slope	slope	-0.22	0.13	-1.67	0.095457387
		Cover*Distance to urban edge	urban_edge_dist:low	-0.89	0.23	-3.81	0.000140992
	Scat: min	Distance to urban edge	urban_edge_dist	1.11	0.16	6.72	1.80E-11
		Cover	high	-18.86	1.03	-18.27	1.41E-74
			low	-17.40	1.21	-14.38	6.44E-47
		Distance to wetland	wetlands_dist	0.19	0.10	1.92	0.054453924
		Distance to coast	coast_dist	-4.58	0.87	-5.24	1.64E-07
		NDVI	ndvi	0.32	0.18	1.80	0.071484209
		Cover*Distance to urban edge	urban_edge_dist:low	-0.56	0.24	-2.29	0.02181199
	Scat: max	Distance to urban edge	urban_edge_dist	1.10	0.16	6.97	3.21E-12
		Cover	high	-19.03	0.98	-19.51	9.18E-85
			low	-18.11	1.23	-14.76	2.67E-49

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
		Distance to coast	coast_dist	-4.92	0.87	-5.63	1.76E-08
		Distance to wetland	wetlands_dist	0.33	0.10	3.41	0.000644948
		Slope	slope	-0.20	0.14	-1.47	0.142914843
		Cover*Distance to urban edge	urban_edge_dist:low	-0.68	0.25	-2.76	0.005784616
	Integrated: scaled	Distance to urban edge	urban_edge_dist	0.27	0.06	4.54	5.53E-06
		Distance to coast	coast_dist	-4.62	0.47	-9.74	2.11E-22
		NDVI	ndvi	0.43	0.09	4.63	3.66E-06
		Slope	slope	0.15	0.07	2.26	0.023659701
		Sex	female	-16.75	0.55	-30.36	1.87E-202
			male	-16.31	0.54	-30.05	2.32E-198
	Integrated: min	Distance to urban edge	urban_edge_dist	0.51	0.08	6.75	1.47E-11
		Distance to coast	coast_dist	-6.17	0.60	-10.28	9.07E-25
		NDVI	ndvi	0.55	0.09	6.08	1.21E-09
		Slope	slope	-0.20	0.09	-2.18	0.029428432
		Sex	female	-19.46	0.82	-23.69	4.72E-124
			male	-18.52	0.80	-23.16	1.07E-118
	Integrated: max	Distance to urban edge	urban_edge_dist	0.38	0.07	5.83	5.68E-09
		Distance to coast	coast_dist	-4.44	0.46	-9.67	3.87E-22
		NDVI	ndvi	0.37	0.08	4.58	4.74E-06
		Sex	female	-16.74	0.53	-31.62	1.79E-219
			male	-16.36	0.53	-30.92	6.05E-210

Appendix 3.5 Top model results for COVER/SEX based on AICc for resting beds and each foraging dataset (prey remains found at GPS clusters, scats, and integrated-diet) and digestion time (minimum, maximum and scaled to prey biomass) for caracals in urban- and wildland-dominated regions of the Cape Peninsula, South Africa.

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
Urban-dominated	Feeding clusters	Distance to urban edge	urban_edge_dist	-4.61	0.78	-5.95	2.74E-09
		Cover	high	-13.99	0.39	-35.45	2.43E-275
			low	-8.72	0.35	-25.25	1.06E-140

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
		Distance to coast	coast_dist	-0.21	0.07	-3.24	0.001189935
		NDVI	ndvi	0.71	0.08	9.11	8.08E-20
		Slope	slope	-0.45	0.10	-4.65	3.30E-06
		Cover*Distance to urban edge	urban_edge_dist:low	11.39	1.10	10.35	4.08E-25
	Scat: scaled	Distance to urban edge	urban_edge_dist	-2.35	0.52	-4.48	7.41E-06
		Cover	high	-12.63	0.23	-55.09	0
			low	-9.78	0.37	-26.27	3.83E-152
		Distance to wetland	wetlands_dist	-0.25	0.08	-3.21	0.001341352
		NDVI	ndvi	0.48	0.07	6.67	2.48E-11
		Slope	slope	-0.26	0.09	-2.84	0.004457768
		Cover*Distance to urban edge	urban_edge_dist:low	7.35	0.96	7.67	1.70E-14
	Scat: min	Distance to urban edge	urban_edge_dist	-2.36	0.53	-4.46	8.36E-06
		Cover	high	-12.64	0.23	-53.88	0
			low	-10.07	0.36	-28.09	1.13E-173
		Distance to wetland	wetlands_dist	-0.27	0.08	-3.47	0.000514854
		NDVI	ndvi	0.46	0.07	6.22	4.83E-10
		Slope	slope	-0.25	0.09	-2.65	0.007979848
		Cover*Distance to urban edge	urban_edge_dist:low	6.69	0.92	7.29	3.13E-13
	Scat: max	Distance to urban edge	urban_edge_dist	-2.38	0.53	-4.47	7.79E-06
		Cover	high	-12.65	0.23	-53.86	0
			low	-10.19	0.34	-29.88	3.39E-196
		Distance to wetland	wetlands_dist	-0.26	0.08	-3.32	0.000893794
		NDVI	ndvi	0.48	0.07	6.46	1.03E-10
		Slope	slope	-0.25	0.09	-2.75	0.00604433
		Cover*Distance to urban edge	urban_edge_dist:low	6.46	0.90	7.15	8.90E-13
	Integrated: scaled	Distance to urban edge	urban_edge_dist	-2.83	0.42	-6.67	2.57E-11
		Cover	high	-12.89	0.20	-65.90	0

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
			low	-9.84	0.26	-38.22	0
		Distance to wetland	wetlands_dist	-0.17	0.06	-3.13	0.001736837
		Distance to coast	coast_dist	-0.14	0.05	-2.89	0.003878946
		NDVI	ndvi	0.52	0.05	9.53	1.63E-21
		Slope	slope	-0.27	0.07	-3.67	0.000246022
		Cover*Distance to urban edge	urban_edge_dist:low	7.24	0.67	10.80	3.53E-27
	Integrated: min	Distance to urban edge	urban_edge_dist	-3.33	0.44	-7.58	3.35E-14
		Cover	high	-13.21	0.21	-63.69	0
			low	-9.38	0.25	-37.35	2.74E-305
		Distance to wetland	wetlands_dist	-0.18	0.06	-3.32	0.000892526
		Distance to coast	coast_dist	-0.11	0.05	-2.38	0.017195187
		NDVI	ndvi	0.63	0.06	11.24	2.49E-29
		Slope	slope	-0.33	0.08	-4.37	1.23E-05
		Cover*Distance to urban edge	urban_edge_dist:low	8.87	0.68	13.02	9.56E-39
	Integrated: max	Distance to urban edge	urban_edge_dist	-1.79	0.39	-4.55	5.35E-06
		Cover	high	-12.57	0.18	-70.50	0
			low	-9.73	0.28	-35.15	1.01E-270
		Distance to wetland	wetlands_dist	-0.21	0.05	-3.90	9.47E-05
		Distance to coast	coast_dist	-0.18	0.05	-3.79	0.000152504
		NDVI	ndvi	0.73	0.06	12.85	8.91E-38
		Slope	slope	-0.26	0.07	-3.67	0.00023992
		Cover*Distance to urban edge	urban_edge_dist:low	5.54	0.65	8.53	1.48E-17
Wildland-dominated	Feeding clusters	Distance to urban edge	urban_edge_dist	0.16	0.09	1.79	0.07276807
		Distance to coast	coast_dist	-7.08	0.92	-7.66	1.84E-14
		NDVI	ndvi	0.67	0.13	4.99	6.05E-07
		Slope	slope	-0.30	0.16	-1.86	0.062384947
		Sex	female	-19.50	1.11	-17.49	1.61E-68

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
			male	-18.84	1.12	-16.77	3.83E-63
	Scat: scaled	Distance to urban edge	urban_edge_dist	1.15	0.16	6.98	2.90E-12
		Cover	high	-19.61	1.07	-18.34	3.70E-75
			low	-18.39	1.23	-14.90	3.13E-50
		Distance to coast	coast_dist	-5.21	0.90	-5.77	7.86E-09
		Distance to wetland	wetlands_dist	0.43	0.11	3.81	0.000137348
		Slope	slope	-0.22	0.13	-1.67	0.095457387
		Cover*Distance to urban edge	urban_edge_dist:low	-0.89	0.23	-3.81	0.000140992
	Scat: min	Distance to urban edge	urban_edge_dist	1.11	0.16	6.72	1.80E-11
		Cover	high	-18.86	1.03	-18.27	1.41E-74
			low	-17.40	1.21	-14.38	6.44E-47
		Distance to wetland	wetlands_dist	0.19	0.10	1.92	0.054453924
		Distance to coast	coast_dist	-4.58	0.87	-5.24	1.64E-07
		NDVI	ndvi	0.32	0.18	1.80	0.071484209
		Cover*Distance to urban edge	urban_edge_dist:low	-0.56	0.24	-2.29	0.02181199
	Scat: max	Distance to urban edge	urban_edge_dist	1.10	0.16	6.97	3.21E-12
		Cover	high	-19.03	0.98	-19.51	9.18E-85
			low	-18.11	1.23	-14.76	2.67E-49
		Distance to coast	coast_dist	-4.92	0.87	-5.63	1.76E-08
		Distance to wetland	wetlands_dist	0.33	0.10	3.41	0.000644948
		Slope	slope	-0.20	0.14	-1.47	0.142914843
		Cover*Distance to urban edge	urban_edge_dist:low	-0.68	0.25	-2.76	0.005784616
	Integrated: scaled	Distance to urban edge	urban_edge_dist	0.27	0.06	4.54	5.53E-06
		Distance to coast	coast_dist	-4.62	0.47	-9.74	2.11E-22
		NDVI	ndvi	0.43	0.09	4.63	3.66E-06
		Slope	slope	0.15	0.07	2.26	0.023659701
		Sex	female	-16.75	0.55	-30.36	1.87E-202

Region	Dataset	Variable	Term	Estimate	Standard error	Statistic	*P*-value
			male	-16.31	0.54	-30.05	2.32E-198
	Integrated: min	Distance to urban edge	urban_edge_dist	0.51	0.08	6.75	1.47E-11
		Distance to coast	coast_dist	-6.17	0.60	-10.28	9.07E-25
		NDVI	ndvi	0.55	0.09	6.08	1.21E-09
		Slope	slope	-0.20	0.09	-2.18	0.029428432
		Sex	female	-19.46	0.82	-23.69	4.72E-124
			male	-18.52	0.80	-23.16	1.07E-118
	Integrated: max	Distance to urban edge	urban_edge_dist	0.38	0.07	5.83	5.68E-09
		Distance to coast	coast_dist	-4.44	0.46	-9.67	3.87E-22
		NDVI	ndvi	0.37	0.08	4.58	4.74E-06
		Sex	female	-16.74	0.53	-31.62	1.79E-219
			male	-16.36	0.53	-30.92	6.05E-210

Appendix 3.6 Top model results for LAND-USE/SEX based on AICc for GPS cluster centroids (for all generated clusters) for caracals in the wildland-dominated region of the Cape Peninsula, South Africa. The caracal group is either the original three individuals considered in this chapter (n = 3) or with two additional individuals included (n = 5).

Group	Variable	Term	Estimate	Standard error	Statistic	*P*-value
Original (n=3)	Distance to urban edge	urban_edge_dist	0.17	0.03	5.69	1.26E-08
	Distance to coast	coast_dist	-2.03	0.08	-26.86	5.74E-159
	Distance to wetland	wetlands_dist	0.07	0.03	2.74	0.006169728
	NDVI	ndvi	0.36	0.02	14.49	1.34E-47
	Slope	slope	0.04	0.02	1.86	0.06252432
	Sex	female	-13.03	0.15	-87.86	0
		male	-12.37	0.19	-65.28	0
	Land-use	plantations	-0.25	0.41	-0.61	0.54230083
		vineyards	-8.06	903.59	-0.01	0.992879823
		altered-open	0.84	0.38	2.18	0.029108903
		urban	-0.51	0.23	-2.19	0.028638051
Additional (n=5)	Distance to urban edge	urban_edge_dist	0.17	0.03	5.90	3.66E-09
	Distance to coast	coast_dist	-1.85	0.07	-27.28	8.17E-164
	Distance to wetland	wetlands_dist	0.08	0.02	3.11	0.001860808

Group	Variable	Term	Estimate	Standard error	Statistic	*P*-value
	NDVI	ndvi	0.37	0.02	15.00	6.99E-51
	Slope	slope	0.04	0.02	1.75	0.079797797
	Sex	female	-12.87	0.23	-56.02	0
		male	-11.71	0.28	-41.19	0
	Land-use	plantations	-0.63	0.39	-1.63	0.102995099
		vineyards	-8.61	956.40	-0.01	0.99281942
		altered-open	0.75	0.38	1.95	0.05076225
		urban	-0.61	0.23	-2.60	0.00939556

Appendix 3.7 Top model results for COVER/SEX based on AICc for GPS cluster centroids (for all generated clusters) for caracals in the wildland-dominated region of the Cape Peninsula, South Africa. The caracal group is either the original three individuals considered in this chapter (n = 3) or with two additional individuals included (n = 5).

Group	Variable	Term	Estimate	Standard error	Statistic	*P*-value
Original (n=3)	Distance to urban edge	urban_edge_dist	0.19	0.03	6.62	3.62E-11
	Distance to coast	coast_dist	-1.94	0.08	-24.81	6.63E-136
	Distance to wetland	wetlands_dist	0.07	0.03	2.61	0.008949969
	NDVI	ndvi	0.40	0.03	13.91	5.48E-44
	Slope	slope	0.04	0.02	2.01	0.044095855
	Sex	female	-13.04	0.15	-86.79	0
		male	-12.38	0.19	-64.18	0
	Cover	low	0.25	0.08	3.12	0.001791608
Additional (n=5)	Distance to urban edge	urban_edge_dist	0.20	0.03	7.01	2.31E-12
	Distance to coast	coast_dist	-1.74	0.07	-25.14	1.91E-139
	Distance to wetland	wetlands_dist	0.07	0.02	2.76	0.005759755
	NDVI	ndvi	0.42	0.03	14.90	3.22E-50
	Slope	slope	0.04	0.02	1.99	0.04710708
	Sex	female	-12.88	0.22	-58.91	0
		male	-11.78	0.27	-43.46	0
	Cover	low	0.32	0.08	4.14	3.50E-05

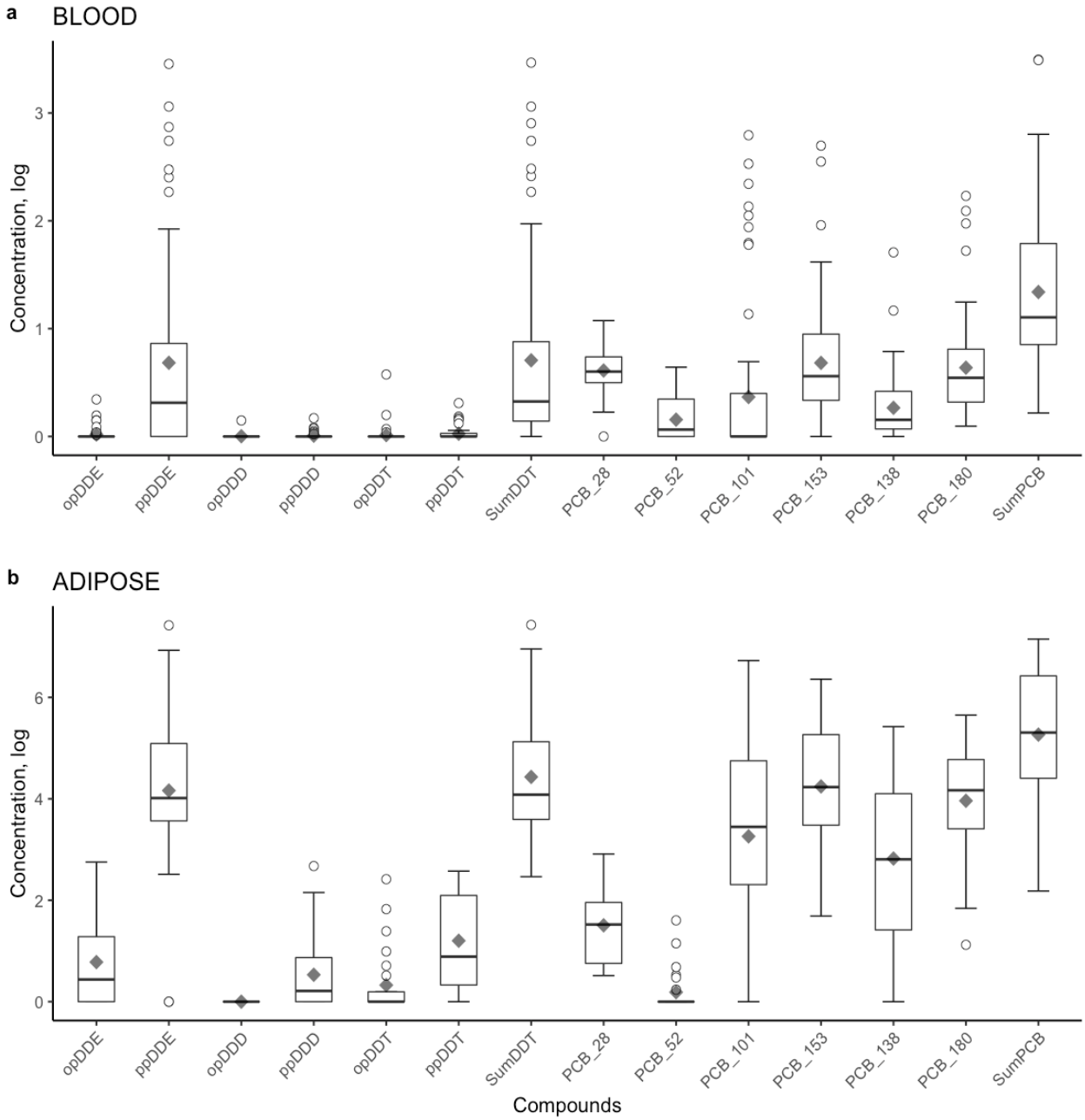
APPENDIX C

Materials for Chapter 4:

Appendix 4.1 Concentrations (ng/g) of organochlorine compounds in tissue (whole blood and adipose) of caracals in the Greater Cape Town area, South Africa in terms of wet weight (w.w.) and lipid weight (l.w.).

Tissue:		Blood (w.w. n = 69, l.w. n = 64)					Adipose (n = 25)				
Compound	Measurement	Mean	SD	Min	Median	Max	Mean	SD	Min	Median	Max
HCB	l.w.	25.55	48.87	0	7.45	270.3	1.24	1.93	0	0.89	9.05
	w.w.	0.05	0.08	0	0.02	0.36	1.1	1.89	0	0.79	8.82
α-HCH	l.w.	16.62	34.51	0	7.65	220.5	0.29	0.41	0	0.14	1.41
	w.w.	0.03	0.04	0	0.03	0.28	0.2	0.26	0	0.12	1.07
β-HCH	l.w.	7.92	25.5	0	0	119.2	1.26	1.82	0	0.41	6.99
	w.w.	0.04	0.14	0	0	1.03	1.03	1.38	0	0.24	4.49
c-HCH	l.w.	13.81	22.86	0	3.8	98.7	7.71	15.4	0	1.6	54.9
	w.w.	0.04	0.06	0	0.02	0.29	5.33	10.8	0	1.29	41.67
d-HCH	l.w.	46.66	98.82	0	14.3	627.2	0.09	0.2	0	0	0.78
	w.w.	0.07	0.08	0	0.06	0.41	0.08	0.17	0	0	0.64
e-HCH	l.w.	2.99	13.94	0	0	89.3	0.67	1.04	0	0.25	4.01
	w.w.	0.01	0.05	0	0	0.33	0.47	0.74	0	0.24	3.25
ΣHCH	l.w.	87.99	124.39	0	42.25	640.8	10.02	16.37	0.28	3.1	58.73
	w.w.	0.19	0.26	0	0.11	1.68	7.11	11.59	0.26	2.72	45.98
Heptachlor	l.w.	10.6	35.71	0	0	260.6	0.04	0.11	0	0	0.51
	w.w.	0.02	0.04	0	0	0.31	0.03	0.09	0	0	0.39
Aldrin	l.w.	3.15	14.87	0	0	113.2	0.01	0.07	0	0	0.34
	w.w.	0.01	0.04	0	0	0.21	0.01	0.06	0	0	0.32
Isodrin	l.w.	34.68	110.56	0	0	637.9	14.33	27.25	0	2.62	96.66
	w.w.	0.11	0.38	0	0	2.56	10.86	19.8	0	2.4	78.25
α-Hepta-epoxide	l.w.	21.48	44.03	0	0	281.7	1.23	3.22	0	0	14.98
	w.w.	0.04	0.11	0	0	0.89	1.15	2.98	0	0	13.82
β-Hepta-epoxide	l.w.	67.63	414.02	0	0	3283.6	1.38	2.42	0	0.37	8.45
	w.w.	0.03	0.08	0	0	0.52	1.1	1.78	0	0.29	6.59
cis-Chlordane	l.w.	5.58	31.7	0	0	245.5	0.95	4.19	0	0	20.85
	w.w.	0.02	0.11	0	0	0.85	0.33	1.22	0	0	5.61
trans-Chlordane	l.w.	4.64	25.56	0	0	201	0	0	0	0	0
	w.w.	0.01	0.02	0	0	0.18	0	0	0	0	0
β-Endosulfan	l.w.	3.46	13.58	0	0	90.2	0.21	0.69	0	0	3.37

Tissue:		Blood (w.w. n = 69, l.w. n = 64)					Adipose (n = 25)				
Compound	Measurement	Mean	SD	Min	Median	Max	Mean	SD	Min	Median	Max
	w.w.	0.01	0.04	0	0	0.2	0.2	0.66	0	0	3.21
o,p'-DDE	l.w.	10.75	33.21	0	0	224.6	3.02	5.33	0	0.57	19.8
	w.w.	0.02	0.06	0	0	0.41	2.39	4.03	0	0.55	14.69
p,p'-DDE	l.w.	1027.04	2485.58	0	142.7	16829.7	232.2	401.57	0	67.02	1751.61
	w.w.	2.41	5.3	0	0.37	30.67	212.09	377.83	0	54.41	1669.79
o,p'-DDD	l.w.	0.45	3.61	0	0	28.9	0	0	0	0	0
	w.w.	0	0.02	0	0	0.16	0	0	0	0	0
p,p'-DDD	l.w.	3.44	10.8	0	0	65	1.54	3.25	0	0.25	14.64
	w.w.	0.01	0.03	0	0	0.18	1.43	3.02	0	0.24	13.5
o,p'-DDT	l.w.	3.84	21.57	0	0	166.8	0.93	2.35	0	0	10.45
	w.w.	0.02	0.1	0	0	0.78	0.89	2.28	0	0	10.19
p,p'-DDT	l.w.	8.67	17.05	0	0	97.5	4.6	5.09	0	1.77	14.98
	w.w.	0.03	0.06	0	0	0.36	3.82	4.03	0	1.43	12.13
ΣDDT	l.w.	1054.19	2492.21	0	170.65	16829.7	242.28	406.29	13.21	69.3	1766.47
	w.w.	2.48	5.36	0	0.38	31.03	220.62	382.42	10.75	58.24	1683.95
PCB-28	l.w.	596.76	1231.7	0	271.85	7702.4	7.25	8.74	0.73	4.13	33.18
	w.w.	0.88	0.36	0	0.82	1.93	5.13	5.22	0.67	3.58	17.39
PCB-52	l.w.	142.27	437.2	0	0	2856.1	0.39	0.98	0	0	4.16
	w.w.	0.19	0.24	0	0.07	0.9	0.35	0.9	0	0	3.97
PCB-101	l.w.	796.03	3876.58	0	5.15	30775.8	121.95	222.43	0	32.17	1028.54
	w.w.	1.12	2.89	0	0	15.34	98.23	173.42	0	30.4	832.68
PCB-153	l.w.	740.95	1570.6	0	315.3	11185.1	160.77	176.16	8.05	94.51	620.48
	w.w.	1.43	2.28	0	0.75	13.83	139.43	159.64	4.41	67.81	576.08
PCB-138	l.w.	184.55	340.12	0	80.35	2312.6	50.46	65.59	0	15.6	244.86
	w.w.	0.38	0.63	0	0.17	4.51	45.58	61.9	0	15.57	225.79
PCB-180	l.w.	688.9	1451.36	12.9	280.55	9063.7	101.02	94.44	6.06	72.11	307.29
	w.w.	1.16	1.51	0.1	0.72	8.31	85.25	79.03	2.07	63.62	283.36
ΣPCB	l.w.	3149.45	6704.16	79.5	1246.4	41860.6	441.84	456.56	24.71	214.56	1591.18
	w.w.	4.27	5.86	0.4	2.02	31.93	368.84	377.77	7.86	200.56	1271.59
Mirex	l.w.	0	0	0	0	0	0	0	0	0	0
	w.w.	0	0	0	0	0	0	0	0	0	0



Appendix 4.2 Boxplots (median, interquartile range, and upper and lower quartile; diamonds = means) of organochlorine compound concentrations (log-transformed) in (**a**) whole blood and (**b**) adipose of caracals in the Greater Cape Town area, South Africa.

Appendix 4.3 Estimates (SE) of top linear mixed effects models (based on AICc) of whole blood organochlorine levels (logged) and spatial predictors in caracal in the Greater Cape Town area, South Africa ($^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$).

Landscape covariates	ΣDDT		ΣPCB		PCB-153		PCB-180	
	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.
Wetlands	0.34*** (0.09)	0.72** (0.33)	0.22*** (0.08)	0.39*** (0.14)	0.17*** (0.06)		0.14*** (0.05)	0.38** (0.15)
Vineyards	0.28*** (0.09)	0.69** (0.32)						
Population density		0.77** (0.34)				0.49** (0.24)		
Constant	0.71*** (0.20)	4.70*** (0.31)	1.40*** (0.19)	7.20*** (0.26)	0.69*** (0.10)	5.40*** (0.24)	0.64*** (0.05)	5.60*** (0.15)
N	69	64	69	64	69	64	69	64

Appendix 4.4 Estimates (SE) of top linear mixed effects models (based on AICc) of adipose organochlorine levels (logged) and spatial predictors in caracal in the Greater Cape Town area, South Africa ($^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$).

Landscape covariates	ΣDDT		ΣPCB		PCB-153		PCB-180	
	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.
Townships	0.87*** (0.20)	0.84*** (0.18)	0.64*** (0.21)	0.60*** (0.18)	0.57*** (0.20)	0.55*** (0.20)		
Transformer density			0.58*** (0.21)	0.47** (0.18)	0.69*** (0.20)	0.62*** (0.20)		
Urban area							0.60*** (0.21)	0.54*** (0.20)
Constant	4.20*** (0.59)	4.40*** (0.46)	5.30*** (0.20)	5.50*** (0.18)	4.20*** (0.20)	4.40*** (0.19)	4.00*** (0.19)	4.20*** (0.20)
N	25	25	25	25	25	25	25	25

Appendix 4.5 Diet proportions in several prey groupings for caracals around Cape Town, South Africa as determined by integrating diet datasets from scat and prey remains found at GPS clusters.

Prey group	Prey category	n	% diet (FO)	% diet (biomass)
Broad taxonomic groups	bird	376	51.44	46.22
	insect	7	0.96	0.08
	mammal	327	44.73	53.25
	reptile	21	2.87	0.45
Functional groups	carnivore	60	8.21	9.63
	granivore	77	10.53	3.08
	herbivore	221	30.23	51.58
	insectivore	37	5.06	0.81
	marine feeder	97	13.27	11.14
	omnivore	239	32.69	23.77
Prey foraging habitat	arboreal	29	3.97	0.78
	ocean	97	13.27	11.14
	terrestrial	401	54.86	71.10
	wetland	204	27.91	16.98
Urban prey groups	exotic	72	9.85	13.76
	synanthropic	183	25.03	27.32
	wild	476	65.12	58.93

Appendix 4.6 Estimates (SE) for top models (based on AICc) of whole blood organochlorine levels (logged) and diet (biomass) for broad taxonomic groups for caracals in the Greater Cape Town area, South Africa ($^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P <$ 0.01).

Variable	ΣDDT		ΣPCB		PCB-153		PCB-180	
	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.
Female	0.64** (0.24)							
Subadult male	-0.09 (0.22)							
Bird biomass					0.16** (0.07)	0.48** (0.23)	0.12* (0.07)	
Insect biomass	-0.23** (0.09)	-0.86** (0.31)	-0.17* (0.10)		-0.12 (0.07)			
Reptile biomass	0.36*** (0.10)	0.75** (0.31)						
Constant	0.37** (0.15)	4.90*** (0.31)	1.20*** (0.10)	7.00*** (0.19)	0.65*** (0.07)	5.60*** (0.23)	0.66*** (0.07)	5.70*** (0.23)
N	34	30	34	30	34	30	34	30

Appendix 4.7 Estimates (SE) for top models (based on AICc) of whole blood organochlorine levels (logged) and diet (FO) for broad taxonomic groups for caracals in the Greater Cape Town area, South Africa ($^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$).

Variable	ΣDDT		ΣPCB		PCB-153		PCB-180	
	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.
Female	0.60** (0.24)							
Subadult male	-0.09 (0.22)							
Bird FO					0.14* (0.07)	0.48** (0.23)	0.13* (0.07)	0.38* (0.22)
Insect FO	-0.30*** (0.10)	-0.72* (0.36)	-0.19* (0.10)					
Reptile FO	0.34*** (0.10)	0.59 (0.36)						
Constant	0.39** (0.16)	4.90*** (0.34)	1.20*** (0.10)	7.00*** (0.19)	0.65*** (0.07)	5.60*** (0.23)	0.66*** (0.07)	5.70*** (0.22)
N	34	30	34	30	34	30	34	30

Appendix 4.8 Estimates (SE) for top models (based on AICc) of whole blood organochlorine levels (logged) and diet (biomass) for prey functional groups for caracals in the Greater Cape Town area, South Africa ($^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$).

Functional group	ΣDDT		ΣPCB		PCB-153		PCB-180	
	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.
Insectivore biomass	0.19* (0.11)							
Herbivore biomass			-0.17* (0.10)		-0.15** (0.07)	-0.59** (0.22)	-0.13* (0.07)	
Carnivore biomass				0.47** (0.18)				0.50** (0.21)
Constant	0.55*** (0.11)	4.90*** (0.36)	1.20*** (0.10)	7.00*** (0.17)	0.65*** (0.07)	5.60*** (0.22)	0.66*** (0.07)	5.70*** (0.21)
N	34	30	34	30	34	30	34	30

Appendix 4.9 Estimates (SE) for top models (based on AICc) of whole blood organochlorine levels (logged) and diet (FO) for prey functional groups for caracals in the Greater Cape Town area, South Africa ($^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$).

Functional group	ΣDDT		ΣPCB		PCB-153		PCB-180	
	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.
Insectivore FO	0.18 (0.11)		0.17* (0.10)					
Herbivore FO			-0.35*** (0.10)	-0.38** (0.18)	-0.23*** (0.07)	-0.66*** (0.20)	-0.18*** (0.07)	-0.51** (0.21)
Carnivore FO		0.72** (0.35)		0.31* (0.18)		0.43** (0.20)		
Marine FO							0.11 (0.07)	
Constant	0.55*** (0.11)	4.90*** (0.34)	1.20*** (0.09)	7.00*** (0.18)	0.65*** (0.07)	5.60*** (0.20)	0.66*** (0.06)	5.70*** (0.21)
N	34	30	34	30	34	30	34	30

Appendix 4.10 Estimates (SE) for top models (based on AICc) of whole blood organochlorine levels (logged) and diet (biomass) for prey foraging habitat for caracals in the Greater Cape Town area, South Africa ($^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$).

Foraging habitat	ΣDDT		ΣPCB		PCB-153		PCB-180	
	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.
Wetland biomass	0.27** (0.10)		0.21** (0.10)		0.14* (0.07)			
Terrestrial biomass							-0.17** (0.07)	
Constant	0.55*** (0.10)	4.90*** (0.36)	1.20*** (0.10)	7.00*** (0.19)	0.65*** (0.07)	5.60*** (0.24)	0.66*** (0.07)	5.70*** (0.23)
N	34	30	34	30	34	30	34	30

Appendix 4.11 Estimates (SE) for top models (based on AICc) of whole blood organochlorine levels (logged) and diet (FO) for prey foraging habitat for caracals in the Greater Cape Town area, South Africa ($^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$).

Foraging habitat	ΣDDT		ΣPCB		PCB-153		PCB-180	
	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.
Wetland FO	0.19* (0.11)							
Terrestrial FO			-0.16 (0.10)				-0.15** (0.07)	
Arboreal FO		-0.67* (0.35)						
Constant	0.55*** (0.11)	4.90*** (0.34)	1.20*** (0.10)	7.00*** (0.19)	0.65*** (0.08)	5.60*** (0.24)	0.66*** (0.07)	5.70*** (0.23)
N	34	30	34	30	34	30	34	30

Appendix 4.12 Estimates (SE) for top models (based on AICc) of whole blood organochlorine levels (logged) and diet (biomass) for exotic prey groups for caracals in the Greater Cape Town area, South Africa ($^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$).

Prey group	ΣDDT		ΣPCB		PCB-153		PCB-180	
	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.
Exotic prey biomass				0.37* (0.19)				0.40* (0.22)
Constant	0.55*** (0.11)	4.90*** (0.36)	1.20*** (0.10)	7.00*** (0.18)	0.65*** (0.08)	5.60*** (0.24)	0.66*** (0.07)	5.70*** (0.22)
N	34	30	34	30	34	30	34	30

Appendix 4.13 Estimates (SE) for top models (based on AICc) of whole blood organochlorine levels (logged) and diet (FO) for exotic prey groups for caracals in the Greater Cape Town area, South Africa ($^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$).

Prey group	ΣDDT		ΣPCB		PCB-153		PCB-180	
	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.
Constant	0.55*** (0.11)	4.90*** (0.36)	1.20*** (0.10)	7.00*** (0.19)	0.65*** (0.08)	5.60*** (0.24)	0.66*** (0.07)	5.70*** (0.23)
N	34	30	34	30	34	30	34	30

Appendix 4.14 Estimates (SE) for top models (based on AICc) of whole blood organochlorine levels (logged) and blood cell count for caracals in the Greater Cape Town area, South Africa ($^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$).

Cell counts	ΣDDT		ΣPCB		PCB-153		PCB-180	
	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.
Total WBC count (x10^9/l)				0.45** (0.22)		0.62** (0.28)		0.46* (0.27)
Lymphocytes (x10^9/l)		0.52 (0.32)	0.14 (0.09)		0.15** (0.06)			
Platelet count (x10^9/l)			0.24** (0.09)		0.18*** (0.06)		0.16** (0.07)	
Constant	0.42*** (0.07)	5.00*** (0.31)	1.10*** (0.08)	7.10*** (0.21)	0.61*** (0.06)	5.60*** (0.27)	0.60*** (0.07)	5.70*** (0.26)
N	30	26	30	26	30	26	30	26

Appendix 4.15 Estimates (SE) for top models (based on AICc) of whole blood organochlorine levels (logged) and serum biochemistry measures for caracals in the Greater Cape Town area, South Africa ($^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$).

Serum biochemistry measures	ΣDDT		ΣPCB		PCB-153		PCB-180	
	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.	w.w.	l.w.
Albumin (g/l)					-0.16** (0.08)			
Albumin:Globulins							-0.15* (0.08)	-0.58* (0.29)
Creatinine (µmol/l)		-0.89** (0.33)	0.19* (0.11)				0.21** (0.09)	
Urea (mmol/l)					0.16** (0.07)			
K+ (mmol/l)		-0.90** (0.34)	-0.23* (0.11)	-0.74*** (0.25)	-0.25*** (0.08)	-0.97*** (0.32)		-0.65** (0.30)
Cl- (mmol/l)	-0.21** (0.08)	-0.69* (0.33)	-0.32*** (0.11)	-0.67** (0.25)	-0.17** (0.08)	-0.92*** (0.32)	-0.18** (0.09)	-0.87*** (0.27)
Constant	0.40*** (0.07)	4.90*** (0.31)	1.10*** (0.10)	7.20*** (0.23)	0.59*** (0.07)	5.60*** (0.29)	0.60*** (0.08)	5.70*** (0.25)
N	23	20	23	20	23	20	23	20

Appendix 4.16 Comparison of DDT concentrations (ng/g) ± SE in wild terrestrial mammalian predators from published studies. Where possible, like tissue was compared with like; where this was not possible, serum/plasma was compared with caracal whole blood and liver/kidney was compared with caracal adipose tissue.

Species	**Caracal**				**Iberian lynx**				**Feral cat**	**Lion**	**Hyena**	**Artic fox**		**Polar bear**			**Brown bear**	**Otter**	
Source	This study				Mateo et al.					Malarvannan et al.		Fuglei et al.	Andersen et al.	Bernhoft et al.	González-Barros et al.	Romanic et al.		Kruuk & Conroy	
Year	2021				2012					2020		2007	2015	1997	2000	2015		1996	
Locality	Cape Town, South Africa				Doñana, Spain		S. Morena, Spain		Doñana, Spain	South Africa		Svalbard, Norway	Svalbard, Norway		Gilicia, Spain	Croatia		Scotland	
n	25	25	69	69	3	6	3	5	2	50	11	20	141	115	12	29	32	116	116
Tissue	adipose		blood		adipose	plasma	adipose	plasma	adipose	serum		adipose	liver	adipose	liver	adipose		liver	
Measure-ment	w.w.	l.w.	w.w.	l.w.	l.w.	w.w.	l.w.	w.w.	l.w.	w.w.	w.w.	l.w.	l.w.	l.w.	l.w.	l.w.	l.w.	w.w.	l.w.
p,p'-DDE	212.09 ± 75.57	232.20 ± 80.31	2.41 ± 0.64	1027.04 ± 310.70	455.00 ± 299.00	1.33 ± 0.48	740.00 ± 234.00	0.31 ± 0.31	1079.00 ± 922.00			154.9 ± 341.40	10.00	372.00	350.00	0.36	0.215	115.00	3988.00
p,p'-DDD	1.43 ± 0.60	1.54 ± 0.65	0.01 ± 0.00	3.44 ± 1.35	<0.01		<0.01		3.35 ± 3.35							<LOD	<LOD		
o,p'-DDT	0.89 ± 0.46	0.93 ± 0.47	0.02 ± 0.01	3.84 ± 2.70											89.00				
p,p'-DDT	3.82 ± 0.81	4.60 ± 1.02	0.03 ± 0.01	8.67 ± 2.13	<0.01		<0.01		16.31 ± 13.77						47.00		<LOD		
∑DDT	220.62 ± 76.48	242.28 ± 81.26	2.48 ± 0.65	1054.19 ± 311.53						0.27 ± 0.33	1.559 ± 5.67				7400.00	0.362	0.232		

Appendix 4.17 Comparison of PCB concentrations (ng/g) ± SE in wild terrestrial mammalian predators from published studies. Where possible, like tissue was compared with like, but where not, serum/plasma was compared with caracal whole blood and liver/kidney was compared with caracal adipose tissue.

Species	Caracal				Iberian lynx				Feral cat	Bobcat	Lion	Hyena	Artic fox				Pole-cat	Polar bear			Wolf				Brown bear	Otter	
Source	This study				Mateo et al.					Boyles & Nielsen	Malarvannan et al.		Fuglei et al.	Andersen et al.	Wang-Andersen et al.		Leonards et al.	Bernhoft et al.	Lie et al.		González-Barros et al.	Shore et al.	Romanic et al.		Kruuk & Conroy	
Year	2021				2012					2017	2020		2007	2015	1993		1994	1997	2005		1997	2001	2015		1996	
Locality	Cape Town, South Africa				Doñana, Spain		S. Morena, Spain		Doñana, Spain	Illinois, USA	South Africa		Svalbard, Norway	Svalbard, Norway	Svalbard, Norway		Netherlands		Svalbard, Norway	Canada	Gilicia, Spain	Russia	Croatia		Scotland	
n	25	25	69	69	3	6	3	5	2	17	50	11	20	141	17	17	7	115	26	30	12	12	58	29	32	116	116
Tissue	adipose		blood		adipose	plasma	adipose	plasma	adipose	liver	serum		adipose	liver	adipose		adipose	adipose	plasma		kidney	liver	liver	adipose		liver	
Measure-ment	w.w.	l.w.	w.w.	l.w.	l.w.	w.w.	l.w.	w.w.	l.w.	l.w.	w.w.	w.w.	l.w.	l.w.	w.w.	l.w.	l.w.	l.w.	w.w.	w.w.	l.w.	l.w.	l.w.	l.w.	l.w.	w.w.	l.w.
PCB-28	5.13 ± 1.04	7.25 ± 1.75	0.88 ± 0.04	596.76 ± 153.96	0.43 ± 0.07		2.11 ± 1.71		2.46 ± 2.17															0.68	0.351		
PCB-52	0.35 ± 0.18	0.39 ± 0.20	0.19 ± 0.03	142.27 ± 54.65		<0.01		0.53 ± 0.53																0.554	0.341		
PCB-101	98.23 ± 34.68	121.95 ± 44.49	1.12 ± 0.35	796.03 ± 484.57	1.90 ± 1.90	<0.01	9.40 ± 9.40	<0.01	72 ± 35.30				3.30 ± 7.80											<LOD	<LOD		
PCB-138	45.58 ± 12.38	50.46 ± 13.12	0.38 ± 0.08	184.55 ± 42.52	50.90 ± 39.00	<0.01	24.00 ± 5.80	<0.01	158.6 ± 129.60	4.60			629.10 ± 674.40	232.00				1330.00						0.778	0.195		
PCB-153	139.43 ± 31.93	160.77 ± 35.23	1.43 ± 0.27	740.95 ± 196.33	124.00 ± 90.00	<0.01	62.00 ± 3.00	<0.01	323.00 ± 262.00	27.20 ±			3056.90 ± 2665.30	2448.00				5930.00				58.60	2.92	0.723			
PCB-180	85.25 ± 15.81	101.02 ± 18.89	1.16 ± 0.18	688.90 ± 181.42	113.10 ± 85.50	0.42 ± 0.27	62.30 ± 3.60	0.29 ± 0.29	238.3 ± 187.40	6.70			2624.20 ± 2535.30	2769.00				3470.00				108.00	2.21	0.372			
Sum PCBs	368.84 ± 75.55	441.84 ± 91.31	4.27 ± 0.71	3149.45 ± 838.02	282.00 ± 266.00	0.42 ± 0.27	202.00 ± 17.00	0.82 ± 0.82	973 ± 736.00	905.00 ± 1107.00	0.00 ± 0.0055	0.03 ± 0.13	9875.10 ± 8786.30	1531.00	8300.00 ± 110000.00	1040 0.00 ± 143000.00	51000.00	15700.00	49.35	42.50	730.00	980.00	450.00	7.12	2.05	797.00	27402.00