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A heavy burden: Metal exposure across the land-ocean continuum in an adaptable carnivore☆

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ABSTRACT

Urbanisation and associated anthropogenic activities release large quantities of toxic metals and metalloids into the environment, where they may bioaccumulate and threaten both wildlife and human health. In highly transformed landscapes, terrestrial carnivores may be at increased risk of exposure through biomagnification. We quantified metallic element and metalloid exposure in blood of caracals (*Caracal caracal*), an adaptable felid inhabiting the rapidly urbanising, coastal metropole of Cape Town, South Africa. Using redundancy analysis and mixed-effect models, we explored the influence of demography, landscape use, and diet on the concentration of 11 metals and metalloids. Although species-specific toxic thresholds are lacking, arsenic (As) and chromium (Cr) were present at potentially sublethal levels in several individuals. Increased use of human-transformed landscapes, particularly urban areas, roads, and vineyards, was significantly associated with increased exposure to aluminium (Al), cobalt (Co) and lead (Pb). Foraging closer to the coast and within aquatic food webs was associated with increased levels of mercury (Hg), selenium (Se) and arsenic, where regular predation on seabirds and waterbirds likely facilitates transfer of metals from aquatic to terrestrial food webs. Further, several elements were linked to lower haemoglobin levels (chromium, mercury, manganese, and zinc) and elevated levels of infection-fighting cells (mercury and selenium). Our results highlight the importance of anthropogenic activities as major environmental sources of metal contamination in terrestrial wildlife, including exposure across the land-ocean continuum. These findings contribute towards the growing evidence suggesting cities are particularly toxic areas for wildlife. Co-exposure to a suite of metal pollutants may threaten the long-term health and persistence of Cape Town's caracal population in unexpected ways, particularly when interacting with additional known pollutant and pathogen exposure. The caracal is a valuable sentinel for assessing metal exposure and can be used in pollution monitoring programmes to mitigate exposure and promote biodiversity conservation in human-dominated landscapes.

1. Introduction

As urban areas continue to expand and rapidly transform natural environments globally (Foley et al., 2005), wildlife are increasingly forced to overcome novel challenges and threats (Ditchkoff et al., 2006; Riley et al., 2014). Anthropogenic threats, including chemical pollution, are a growing global concern (Persson et al., 2022), and both cities and rapidly developing countries are disproportionately affected due to extensive industrial activity and land-use change (Landrigan et al., 2017). Environmental chemical pollutants often go undetected by wildlife, and prolonged exposure results in their accumulation in body fluids and tissues (Ortiz-Santaliestra et al., 2015) with potentially lethal and sublethal effects (Desforges et al., 2016; Huang et al., 2018; Sonne et al., 2020). Consequences of exposure include neurological and endocrine disruption, reproductive impairment, immunosuppression, and increased susceptibility to disease (Scheuhammer et al., 2007;

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Acevedo-Whitehouse & Duffus, 2009). Urban wildlife are at particular risk of pollutant exposure as they are likely to feed within synanthropic food webs and utilise human-transformed habitats (Elliott et al., 2015; Guetté et al., 2017).

Among the most ubiquitous, toxic, and well-studied chemical pollutants are metals and metalloids. Heavy metals, including cadmium (Cd), chromium (Cr), mercury (Hg) and lead (Pb), and metalloids like arsenic (As) are high-density chemical elements, which may become toxic even at low concentrations (Duffus, 2001; Mitra et al., 2022). Anthropogenic point sources include coal power plants, mines, and waste disposal sites (e.g., landfills or illegal dumping sites; Hernández et al., 2017; Custodio et al., 2020). Further, lead exposure in wildlife may also occur due to spent hunting ammunition (Burco et al., 2012) and contamination through use of agricultural areas (Soliman et al., 2019). Some metals persist for long periods of time (Scheifler et al., 2006). Moreover, the trophic transfer of metals means that species that are spatially removed from polluted sites may still become contaminated (Soliman et al., 2022). Wildlife are typically exposed through dietary pathways (Gall et al., 2015) and, accordingly, toxic metal levels in wildlife have been linked to food webs in urban and agricultural areas (Souza et al., 2013).

While many metals originate from anthropogenic point sources, aquatic environments generally act as sinks, which accumulate these elements (Weiss-Penzias et al., 2019). Due to anoxic conditions in water, metals may be converted into more toxic and bioavailable forms (e.g., mercury into methylmercury) and can be readily taken up by biota and biomagnified up and across food webs (Gobas et al., 1993). Therefore, aquatic species and those with aquatic-based diets may be at higher risk of exposure to certain metals (Ishii et al., 2017), where contamination within marine and freshwater food webs can spillover into terrestrial food webs (Cristol et al., 2008). This phenomenon is well-documented in North American river otters (*Lontra canadensis*) and wild mink (*Mustela vison*), whose high mercury burdens have been linked to their predominately fish-based diet (Yates et al., 2005), resulting in neurotoxic effects in both species (Basu et al., 2005a; Basu et al., 2005b).

Carnivores contribute important top-down trophic effects in ecosystems (Ripple et al., 2014), but in doing so they are disproportionately exposed to pollutants in transformed landscapes through biomagnification (Millán et al., 2008; Bateman & Fleming, 2012). Accordingly, carnivores are important bioindicators for assessing transfer of pollutants in both terrestrial and aquatic ecosystems (Bossart, 2011; Bocharova et al., 2013; Harley et al., 2016). Large carnivores are largely absent from cities (Cardillo et al., 2004), but many small and medium-sized carnivores (i.e., 'mesocarnivores'), such as coyote (*Canis latrans*; Lombardi et al., 2017) and bobcat (*Lynx rufus*; Riley et al., 2003) are more resilient to the novel challenges faced in urbanised spaces (Crooks, 2002; Bateman & Fleming, 2012), particularly where there are opportunities for enhanced resource exploitation (Larson et al., 2020; Hody & Kays, 2018). However, using urban environments may also expose species to greater risks, including human-wildlife conflict, and exposure to disease and harmful pollutants (Moss et al., 2016; Murray et al., 2019). Wildlife may also be subject to an 'ecological trap' (Dwernychuk & Boag, 1972), where animals misinterpret novel urban cues and prefer a low-quality habitat over other available habitats of higher quality (Battin, 2004). Rapid environmental change can promote the emergence of ecological traps, as animals have less time to learn and adapt to changing cues, resulting in habitat selection errors with fitness consequences (Kokko & Sutherland, 2001; Schlaepfer et al., 2002; Sievers et al., 2018). Mesocarnivores in urban areas may be useful indicator species to understand this phenomenon, particularly in the Global South where there are large knowledge gaps (Zuñiga-Palacios et al., 2021).

In this study we quantified circulating levels of metals and metalloids in blood samples from an urban-adapted population of caracals in Cape Town, South Africa. Caracals (*Caracal caracal*) are medium-sized, generalist felids. In Cape Town, the species appears to have adapted to living on the urban edge of this rapidly urbanising, coastal metropole (Leighton et al., 2021), but they are also widely exposed to numerous toxicants, including rodenticides (Serieys et al., 2019) and organochlorines (Leighton et al., 2022) through dietary and landscape use pathways. We hypothesised that demographic characteristics and the foraging ecology of these caracals significantly influence individual exposure and body burden of metals and metalloids. We tested this using a detailed analysis of metal blood concentrations together with age, sex, habitat use, diet, and haematological analysis variables. We discuss our findings in the challenging framework of carnivore persistence in rapidly urbanising landscapes and consider possible mitigation strategies and future research directions based on the exposure pathways we uncover.

2. Materials and methods

2.1. Study area

Caracals occurring in and around the metropole of the City of Cape Town (hereafter the Greater City of Cape Town, GCT), Western Cape, South Africa (−33.942989, 18.630957) were sampled and tested for exposure to 11 metals and metalloids. The GCT spans ~470 km^2 with an estimated human population of 4.8 million, with ~1530 people per km^2 (worldpopulationreview.com). The area comprises a mosaic of human-transformed and natural areas, with a strong north–south urban gradient (Fig. 1). The dominant land-use types are urban areas (including formal and informal housing and industrial areas), agricultural (including vineyards, pine and eucalyptus plantations, and orchards), and natural land (mostly shrubland fynbos). A significant portion (~220 km^2) of the GCT's physical landscape includes Table Mountain National Park (TMNP), a natural protected area, dominated by the Table Mountain Chain and a coastline of >300 km (Western Cape Government (WCG), 2019). Most of the southern Peninsula is protected in the Cape Point section of TMNP. The Cape Peninsula is almost entirely bounded by the Atlantic Ocean and by urban sprawl to the east (Fig. 1).

2.2. Capture and sampling of caracals

Standard cage-trapping techniques were used to humanely capture and GPS-collar caracals between 2014 and 2017 under veterinary supervision (detailed capture and collaring method described in Leighton et al., 2022). Samples were also opportunistically collected from caracal carcasses which were collected from throughout the study area and stored at −20 °C until necropsy. A total of 67 blood samples were taken during captures, recaptures, and necropsies of 53 unique individuals (Table 1) and stored at −20 °C in cryotubes (Greiner Bio-One Cryo. s™ Tubes). Comprehensive haematological and serum biochemistry analyses were carried out by Vet Diagnostix (pathology services, Cape Town, South Africa) or by Penzance Veterinary Clinic (Cape Town, South Africa). Animal capture, handling, and sampling protocols followed ethical guidelines approved by the American Society of Mammalogists and the University of Cape Town Animal Ethics Committee (2014/V20/LS). Samples were collected under permits from Cape Nature (AAA007-0147-0056), and South African National Parks (SERL/AGR/017–2014/V1).

2.3. ICP-MS elemental analysis

This study focuses on 11 chemical elements commonly analysed in wildlife studies, including heavy metals (cadmium, chromium, mercury and lead), other metallic elements (aluminium, cobalt, copper, manganese, and zinc) and metalloids (arsenic and selenium). Metals and metalloids were selected based on the following criteria: (i) their relative level of toxicity and potential to cause adverse health effects in wildlife and humans; (ii) those metals that are the focus of other relevant

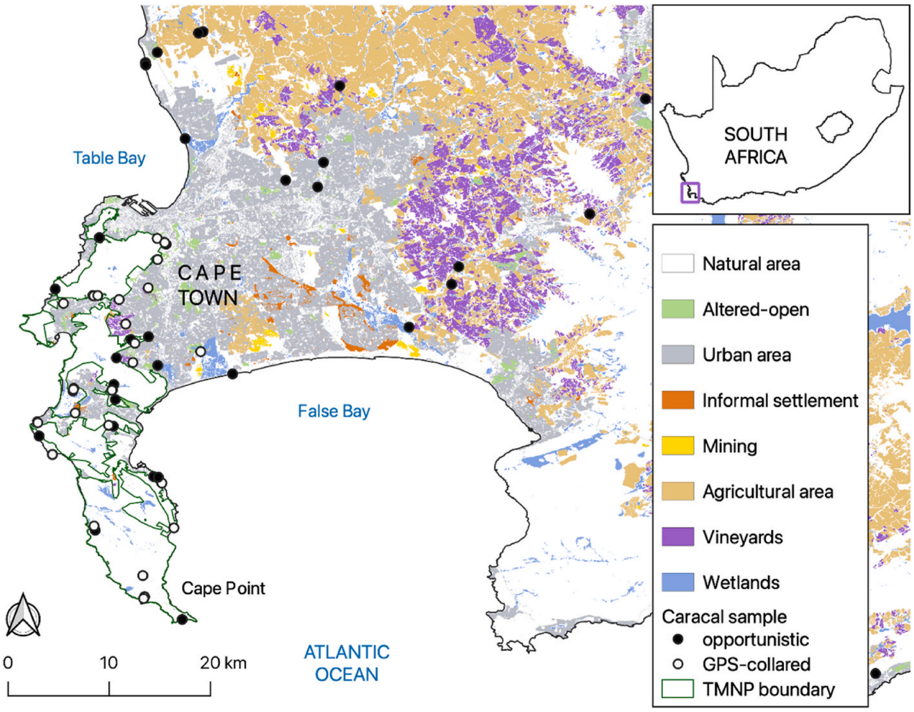

Fig. 1. Map showing locations of individual caracals sampled for metals and metalloids in the Greater Cape Town area, South Africa. White circles represent locations of caracal individuals that were trapped and monitored with GPS collars, and therefore have estimated home ranges. Black circles are opportunistically sampled individuals with buffers calculated around collection locations. Coloured areas correspond to different land-uses. The green line denotes the Table Mountain National Park (TMNP) boundary.

Table 1
Caracal samples tested for metal and metalloid exposure in the Greater City of Cape Town, South Africa (n = 53 individuals). Due to low sample size, adult (n = 17) and subadult (n = 6) females were considered together as “females”.

Sampling	Demographic group	Total (n = 67)	Captures (n = 29)	Recaptures (n = 6)	Mortalities (n = 32)
GPS-collared (n = 47)	Juvenile male	14	9	0	5
	Adult male	17	9	4	4
	Female	16	10	2	4
Opportunistic (n = 20)	Juvenile male	9	0	0	9
	Adult male	4	0	0	4
	Female	7	1	0	6

literature on metal exposure in carnivores; and (iii) metals with an established association with human-transformed landscapes. Metal concentrations were determined in caracal whole blood using Inductively Coupled Plasma Mass Spectrometry (ICP-MS). Blood samples were lyophilised (−55 °C; Christ Alpha 1–2, Braun Biotech) and 100 mg was weighed into microwave vessels with 1 ml of HNO_3, 1 ml of H_2O_2 and 11 ml of H_2O (Milli-Q grade), and then placed in a microwave oven (Ethos E, Milestone). For 1.5 min samples were ramped up from ambient temperature to 85 °C, held at 135 °C for 2 min, then for a further 1.5 min at 230 °C and held at this temperature for 15 min. Digested samples were then diluted to a final volume of 50 ml with Milli-Q H_2O and analysed on an ICP-MS (Agilent 7800, Agilent Technologies, United States) using an autosampler SPS 4. Finally, the samples were analysed with ISIS (Integrated Sample Introduction System) at RF 1550 W at 100 sweeps/replicate. Blanks and certified reference materials (ERM-CE196 Bovine blood [Joint Research Centre] and TORT-3 Lobster hepatopancreas [National Research Council of Canada]) were digested and analysed with each batch (n = 5) of samples. The recoveries obtained with ERM-CE196 were 106.9 ± 16.2% for cadmium and 102.7 ± 2.0% for lead; and with TORT-3 were 112.2 ± 2.8% for arsenic, 101.4 ± 2.9% for cadmium, 80.1 ± 3.0% for copper, 85.9 ± 5.0% for chromium, 71.3 ± 5.9% for mercury, 88.4 ± 4.5% for manganese, 107.5 ± 2.8% for selenium, 74.1 ± 3.2% for lead and 93.9 ± 2.9% for zinc. The limits of detection (LOD, in μg/g dry weight (d.w.) of sample) for all metals were as follows: 0.244 (aluminium), 0.002 (arsenic), 0.001 (cadmium), 0.026 (copper), 0.002 (cobalt), 0.018 (chromium), 0.002 (mercury), 0.004 (manganese), 0.077 (selenium), <0.001 (lead), and 0.019 (zinc). Metal concentrations are reported in μg/g d. w.

2.4. Statistical analysis

i. Landscape use and associated risk factors for metal exposure

We tested whether certain land-use types (e.g., urban, agriculture, or mining; Table S1) were associated with variation in metal concentrations in caracal blood. Proximity to the coast was also tested because terrestrial species may be exposed to metals and metalloids including arsenic, mercury, selenium and cadmium when feeding within marine food webs (Scheuhammer et al., 2007; Dietz et al., 2022). Caracal land-use was measured within 95% Local Convex Hull home ranges estimated using the spatial movement data (n = 36; see Leighton et al., 2022). For opportunistically sampled caracals (n = 31), land-use variables were calculated within a circular buffer around the GPS location where the individual was found, following Leighton et al. (2022). Previous research has found that caracal home ranges significantly varied amongst sex and age classes (Leighton et al., 2021), therefore different buffer sizes were assigned for females (mean home range = 16.2 km^2), adult males (69.9 km^2) and subadult males (38.3 km^2). The land-use types considered were the proportion urban, agricultural, vineyard, wetland, informal settlement, mining, natural area, and altered-open area using the 2018 Department of Environmental Affairs (DEA) national land-cover raster. Altered-open areas included urban recreational fields, golf courses, fallow land and old fields, abandoned quarries and landfill sites. Additionally, we included the mean distance from the coast, human population density, and road density (see Table S1 for details). Binary rasters were created for each land-use type, and density rasters for human population and roads (Table S1). The proportion of each land-use variable, the mean distance to coast, and the mean population and road density within individual caracal home range polygons or buffer circles were then calculated.

ii. *Dietary risk factors for metal exposure*

We used a detailed dietary dataset (Table S2; Leighton et al., 2020), which integrates both scat and caracal feeding sites located at GPS clusters of collared individuals to investigate which dietary pathways hold the highest metal exposure risks. Diet proportions were based on both biomass (BIO) and frequency of occurrence (FO) of prey per caracal individual (Table S2). Dietary patterns were assessed by assigning prey into different groups and calculating their proportion in diet, categorised as follows: broad food groups (proportion bird, mammal, reptile, insect), prey functional groups (carnivore, insectivore, granivore, herbivore, omnivore, and marine feeder), prey foraging habitat type (i.e., in terrestrial, wetland, arboreal and marine environments), and level of human association (i.e., wild, exotic, or synanthropic prey) groups. Exotic prey included introduced species, domestic animals, and livestock. Synanthropic prey are indigenous, wild species that live close to and benefit from humans (Guetté et al., 2017).

iii. *Haematological, serum chemistry, and body condition parameters*

We tested for possible physiological or stress responses to metallic element and metalloid exposure using blood pathology data as in Leighton et al. (2022). Caracals with higher exposure may have consequently lower body condition and increased measures of being immunocompromised or stressed (Davis et al., 2008; Murray et al., 2019). We obtained detailed haematological analysis for collared individuals, including complete cell counts (total white and red blood cell count, neutrophil, lymphocyte, eosinophil, monocyte, basophil and platelet count, haemoglobin, mean corpuscular volume (MCV), mean corpuscular haemoglobin concentration (MCHC) and red cell distribution width) and serum biochemistry (total serum protein, albumin, globulins, albumin:globulin ratio, alanine transaminase (ALT), alkaline phosphatase (ALP), total bilirubin, urea, creatinine, phosphate, $Cl-$, $Na+$, $K+$ concentration and Na:K ratio). 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 we 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). We also calculated a body condition index (BCI) based on an Ordinary Least Squares method (OLS; Labocha et al., 2014) of body length and weight, 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 age and sex.

iv. Redundancy analysis

To assess the effects of land-use on metal concentrations we first performed a detrended correspondence analysis (DCA) using the *vegan* package in R. This analysis revealed a gradient length of <3 for axis 1, thus, we used a model with a linear response curve (Ortiz-Santaliestra et al., 2015). Next, we conducted a redundancy analysis (RDA) to understand the broad influence of land-use explanatory variables on all caracal blood metal concentrations (ter Braak, 1994). Due to insufficient sample size ($n = 34$), dietary variables were not included. We assessed multicollinearity in all land-use explanatory variables (Table S1) and retained only those considered independent (VIF <8.5; Vittinghoff et al., 2012; James et al., 2013). Continuous explanatory variables were scaled (by 1 SD) and centred. Final models were selected using AICc scores. Significance testing of explanatory covariates was performed using a Monte Carlo Permutation test (1000 permutations).

v. Linear and linear mixed-effects models: demographic, land-use, and dietary variables

To investigate which variables best explained variation in the elements of interest (i.e., metal concentration as the response variable), we ran linear mixed-effects models with demography (i.e., age class and sex groups; Table 1) and land-use as explanatory variables, and linear models with dietary and haematological explanatory variables (i.e., cell counts and serum biochemistry) variables (Tables S4–S14). As concentrations were non-normal (Shapiro-Wilk's $P < 0.001$), we natural log-transformed the data. We then used AICc scores to identify the best model based on all combinations of the subset of relevant predictor variables selected. To incorporate all caracal samples (those with known home ranges and opportunistically sampled) we 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 $= 0$) in land-use RDA and linear models where necessary (i.e., for cadmium, mercury, manganese and selenium models). To avoid singularity, this random effect was not included in all models, as some datasets were unaffected (random effect variance $= 0$). All statistical analyses were performed in R version 4.1.0 (R Core Team, 2022).

3. Results

3.1. *Caracal exposure to metals in study area*

A total of 67 caracal blood samples (representing 53 unique individuals) were collected across the study area (Table 1). Most resampling was between 6 months to a year apart (mean = 10 months), usually sampling from capture to mortality.

Metal and metalloid concentrations varied between individuals of the Greater City of Cape Town caracal population by as much as two orders of magnitude between means in certain elements (Table 2; Fig. S1). Mean concentrations of the 11 elements in descending order were as follows: zinc > aluminium > copper > manganese > arsenic > selenium > mercury > chromium > cadmium > lead > cobalt.

3.2. *Land-use and demographic risk factors*

Together, land-use variables in the initial RDA model (Table S3) explained approximately 18.6% of the total variation in metal

Table 2
Summary of whole blood metal and metalloid concentrations (mean ± SD; μg/g d.w.) of caracals in and around the Greater City of Cape Town area, South Africa.

Metals and metalloids	Mean	Median	Range
Aluminium (Al)	7.70 ± 25.57	1.16	0.12–147.08
Arsenic (As)	3.74 ± 8.38	1.17	0.04–54.82
Cadmium (Cd)	0.06 ± 0.14	0.001	0.001–0.76
Cobalt (Co)	0.01 ± 0.01	0.003	0.001–0.04
Chromium (Cr)	0.29 ± 0.76	0.14	0.01–5.16
Copper (Cu)	5.88 ± 5.66	3.47	0.31–36.08
Mercury (Hg)	0.45 ± 0.74	0.17	0.001–3.84
Manganese (Mn)	3.84 ± 1.79	0.18	0.02–7.33
Lead (Pb)	0.03 ± 0.03	0.02	0.01–0.23
Selenium (Se)	3.69 ± 1.55	3.41	0.25–9.03
Zinc (Zn)	56.55 ± 54.18	35.99	2.31–322.79

concentrations across caracal samples. Forward selection of this model revealed “vineyards” and “distance from coast” were the top predictor variables (Fig. 2), explaining a combined 11.5% of total variation. Therefore, we selected these two variables to build our final RDA model (Table S3). The final model was significant ($F_{2,63} = 4.11$, $P < 0.05$) with a total inertia of 3.73 (0.40 constrained, 3.3 unconstrained). The RDA analysis generates axes that represent linear combinations of the explanatory variables (i.e., land-use variables; Legendre & Legendre, 2012). The first RDA axis (RDA1) explained 8.87% of total variation and the second RDA axis (RDA2) explained 2.68% (Fig. 2).

Nine (aluminium, arsenic, cobalt, chromium, copper, mercury, lead, selenium and zinc) of the 11 elements modelled showed a significant or marginally significant association with at least one land-use type (Fig. 3A; Table S4). With increasing proportion of urban area in home ranges and buffers, caracals had higher aluminium ($\beta = 0.30 \pm 0.13$, $P < 0.05$; Fig. 3A) levels in blood. Increased road density in home ranges and buffers was associated with a marginal increase in caracal blood levels of cobalt ($\beta = 0.002 \pm 0.001$, $P = 0.05$) and lead ($\beta = 0.006 \pm 0.0038$, $P = 0.07$) and lowered blood levels of arsenic ($\beta = -0.35 \pm 0.11$, $P < 0.05$). The use of agricultural land had a negative influence on levels of arsenic ($\beta = -0.34 \pm 0.14$, $P < 0.01$) and selenium ($\beta = -0.15 \pm 0.03$, $P < 0.01$). Increased use of vineyards was associated with elevated caracal blood levels of arsenic ($\beta = 0.28 \pm 0.14$, $P < 0.05$) and lowered blood levels of copper ($\beta = -0.26 \pm 0.07$, $P < 0.01$) and zinc ($\beta = -0.37 \pm 0.11$, $P < 0.01$). Caracals using areas closer to the coast had lower blood levels of copper ($\beta = 0.21 \pm 0.07$, $P < 0.05$), marginally lower levels of zinc ($\beta = 0.21 \pm 0.11$, $P = 0.06$) and higher levels of mercury ($\beta = -0.12 \pm 0.04$, $P < 0.05$). A greater proportion of informal settlements in home ranges and buffers was associated with elevated cobalt ($\beta = 0.002 \pm 0.001$, $P < 0.05$), while human population density was positively associated with elevated levels of chromium ($\beta = 0.07 \pm 0.03$, $P < 0.05$). The use of altered-open land had a negative influence on selenium levels ($\beta = -0.09 \pm 0.04$, $P < 0.05$). No significant relationships were found between any metal and wetlands or mining land-uses. Cadmium was not significantly associated with any land-use type (Table S4). Juvenile male caracals showed elevated levels of arsenic ($\beta = 0.78 \pm 0.25$, $P < 0.05$) and manganese ($\beta = 0.5 \pm 0.18$, $P < 0.05$), as well as cobalt ($\beta = 0.004 \pm 0.002$, $P = 0.09$) and copper ($\beta = 0.31 \pm 0.15$, $P = 0.05$), although the latter was marginally significant. There was no other effect of demographic group on metal concentrations.

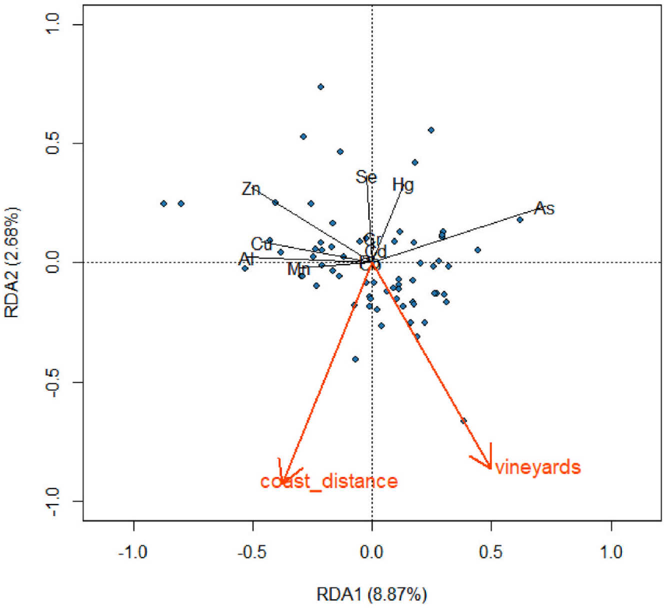

Fig. 2. Triplot showing results of RDA analysis and Monte Carlo permutation test to analyse the effect land-use variables (orange arrows) have on logged blood metallic element and metalloid concentrations (black lines) in caracals. Blue diamonds represent caracal samples. The first canonical axis (RDA1) is shown on the x-axis and the second (RDA2) on the y-axis. Percentage of variance explained are shown in each axis. Only significant variables are shown.

3.3. *Dietary exposure risks*

Using detailed dietary datasets, we explored metal exposure risks for caracals through different dietary pathways (see full top model outputs in Tables S5–S12).

i. Broad prey groups

Caracals with a greater proportion of avian prey in their diet had marginally higher blood concentrations of arsenic ($\beta = 0.25 \pm 0.13$ BIO, $P = 0.05$; Fig. 4A) and mercury ($\beta = 0.09 \pm 0.05$ BIO, $P = 0.09$; $\beta = 0.09 \pm 0.05$ FO, $P = 0.08$; Fig. 4B). The most frequently consumed avian species included Cape cormorants (*Phalacrocorax capensis*), Guinea fowl (*Numida meleagris*) and Egyptian geese (*Alopochen aegyptiaca*). Avian species made up a relatively large proportion of total caracal diet (46% BIO; 51% FO; Table S2). An increase in the proportion of insects in diet was marginally associated with increased caracal exposure to aluminium ($\beta = 0.37 \pm 0.19$ BIO, $P = 0.06$) and influenced exposure to cobalt ($\beta = 0.002 \pm 0.0009$ BIO, $P < 0.05$; $\beta = 0.0021 \pm 0.001$ FO, $P < 0.01$), particularly in juvenile males ($\beta = 0.047 \pm 0.002$ BIO, $P < 0.05$). However, insects made up the smallest proportion of all prey groups (0.08% BIO; 0.96% FO).

ii. Prey functional groups

An increase in the proportion of carnivorous species in caracal diet was linked to a marginally elevated level of aluminium in terms of biomass ($\beta = 0.35 \pm 0.19$ BIO, $P = 0.07$) and significantly elevated in terms of FO ($\beta = 0.45 \pm 0.19$ FO, $P < 0.05$), particularly in the blood of juvenile males ($\beta = 1.05 \pm 0.46$ FO, $P < 0.05$). An increase in the proportion of carnivore ($\beta = -0.27 \pm 0.13$ BIO, $P < 0.05$) and herbivore ($\beta = -0.35 \pm 0.13$ BIO, $P < 0.01$) prey functional groups was correlated with a decrease in blood concentration of arsenic (Fig. 3C). Herbivores made up the largest proportion of prey consumed by caracals, on average (51.5% BIO; 30.2% FO; Table S2), while carnivorous prey was far lower (9.6% BIO; 8.2% FO). An increase in preying on marine-feeders was associated with increased selenium in blood ($\beta = 0.07 \pm 0.04$ BIO, $P = 0.06$; $\beta = 0.08 \pm 0.05$ FO, $P < 0.05$; Fig. 3C). The majority of marine prey species were seabirds (marine feeders: 11.14% BIO, 13.27% FO; Table S2), mainly Cape cormorants. An increase in the frequency of occurrence of herbivorous prey species was associated with decreased caracal blood concentration of mercury ($\beta = -0.13 \pm 0.05$ FO, $P < 0.01$) and arsenic ($\beta = -0.35 \pm 0.13$ BIO, $P < 0.01$).

iii. Prey foraging habitat

An increase in the proportion of wetland-adapted species in diet was linked with an increase in arsenic ($\beta = 0.27 \pm 0.13$ BIO, $P < 0.05$), mercury ($\beta = 0.16 \pm 0.05$ BIO, $P < 0.05$, $\beta = 0.11 \pm 0.05$ FO, $P < 0.05$) and selenium ($\beta = 0.09 \pm 0.04$ BIO, $P < 0.01$; $\beta = 0.08 \pm 0.03$ FO, $P < 0.05$). There was also a marginally significant increase in the concentration of copper ($\beta = 0.18 \pm 0.09$ BIO, $P = 0.06$), manganese ($\beta = 0.16 \pm 0.09$ BIO, $P = 0.07$) and zinc ($\beta = 0.21 \pm 0.13$ BIO, $P = 0.09$) in the blood of caracals feeding on more wetland-adapted species (Fig. 3B). Wetland-adapted species mainly included Egyptian goose, African sacred ibis (*Threskiornis aethiopicus*), and vlei rat (*Otomys irroratus*; Table S2: 16.98% BIO; 27.91% FO). Caracal blood concentration of mercury ($\beta = 0.09 \pm 0.04$ BIO, $P < 0.05$, $\beta = 0.13 \pm 0.05$ FO, $P < 0.05$; Fig. 4C) and selenium ($\beta = 0.09 \pm 0.04$ BIO, $P < 0.01$, $\beta = 0.11 \pm 0.03$ FO, $P < 0.05$; Fig. 4D) was associated with increased feeding on marine-adapted species (Table S2:11.14% BIO; 13.27% FO). The main marine-

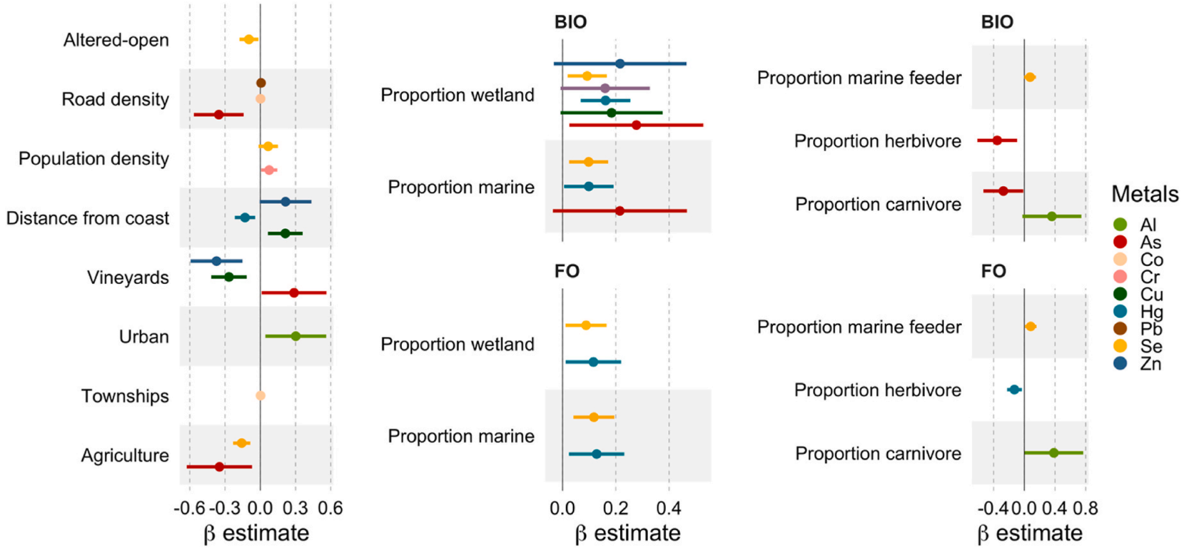

Fig. 3. Coefficient estimates and 95% confidence intervals for (**A**) linear mixed-effects models of land-use variables, and (**B–C**) linear models for dietary variables for biomass (BIO) and frequency of occurrence (FO) estimates (see Materials and methods), with concentration of metals and metalloids in caracal whole blood as the response variable. Only significant top parameters (as determined by AICc) are shown. Elements are reported in alphabetical order.

adapted species included seabirds like Cape cormorants and gulls. No significant associations were found for arboreal prey groups.

iv. Exotic prey group

Caracals had lower blood levels of arsenic ($\beta = -0.30 \pm 0.12$ BIO, $P < 0.05$; $\beta = -0.22 \pm 0.12$ FO, $P = 0.07$) and selenium ($\beta = -0.08 \pm 0.04$ BIO, $P < 0.05$; $\beta = -0.06 \pm 0.08$ FO, $P = 0.08$) when feeding on more synanthropic prey species. Synanthropic species were mainly Guinea fowl and Egyptian geese (Table S2; 27.3% BIO; 25% FO). No significant associations were found for the exotic or wild prey groups.

3.4. *Physiological condition and metal element exposure*

We tested for potential relationships between metals and metalloids and blood measures to investigate physiological responses to exposure. Lymphocyte count was marginally significantly elevated in individuals with higher selenium blood concentration ($\beta = 0.09 \pm 0.04$, $P = 0.05$; Table S13). Further, platelet count was significantly higher in individuals with higher mercury ($\beta = 0.11 \pm 0.04$, $P < 0.01$) and selenium levels (although this was marginally significant, $\beta = 0.08 \pm 0.04$, $P = 0.06$; Table S13), indicating a response to potential infection or inflammation (i.e., potentially triggering immunologic or inflammatory mechanisms). Mean corpuscular volume (MCV) was elevated in individuals with higher levels of aluminium ($\beta = 0.44 \pm 0.16$, $P < 0.01$) and lead (although this was marginally significant, $\beta = 0.01 \pm 0.01$, $P = 0.06$). Notably, mean corpuscular haemoglobin concentration (MCHC) was significantly lower in individuals with higher levels of chromium ($\beta = -0.13 \pm 0.05$, $P < 0.05$), mercury ($\beta = -0.10 \pm 0.04$, $P < 0.05$), manganese ($\beta = -0.04 \pm 0.02$, $P = 0.05$), and zinc ($\beta = -0.21 \pm 0.1$, $P < 0.05$; Table S13), while haematocrit was within normal range (30–45% packed cell volume, PCV) for the majority (>86%) of individuals, potentially indicating hypochromic anaemia. Serum biochemistry analysis suggests that exposure to metals and metalloids reduces chlorine (Cl-), potassium (K+), sodium (Na+) and albumin levels (Table S14). There was also some evidence that cobalt contamination decreased creatinine ($\beta = -0.000498 \pm 0.000215$, $P < 0.05$) and arsenic increased phosphates ($\beta = 0.32 \pm 0.15$, $P < 0.05$). However, it should be noted that sample size was relatively low for these serum biochemistry models (Table S14, n = 23). There were no significant patterns seen with metal levels and body condition for either the OLS residuals or SMI methods ($P > 0.05$; n = 51).

4. Discussion

Our study reveals significant roles for demography, landscape use and diet in the exposure of certain metals in caracals inhabiting the city of Cape Town, South Africa. Notably, exposure pathways varied between metals; greater use of human-transformed landscapes was associated with increased levels of aluminium, arsenic, cobalt, and lead, while exploiting both marine and terrestrial aquatic food webs increased exposure to arsenic, mercury, and selenium. The blood concentration dataset reported here contributes to our understanding of the threat that metal pollution poses to terrestrial carnivores persisting in human-transformed landscapes; this is particularly important in the Global South where data is lacking (Rodríguez-Estival and Mateo, 2019) and can be used as a baseline to test for future fluctuations in metal exposure in South Africa's rapidly urbanising cities.

4.1. *Potential physiological consequences of exposure*

Due to a lack of species-specific thresholds for metal concentrations in caracals, our findings are compared to literature from other terrestrial carnivores (see Table S15). Most elements in our study (>80%) were detected below established toxic concentrations in mammals, apart from arsenic and chromium which may represent sublethal levels in certain individuals (Table S15). Accordingly, there may because for concern, given that caracals are also exposed to toxic anticoagulant rodenticides (Serieys et al., 2019) and organochlorines (Leighton et al., 2022), which may act in concert with high metal burdens with likely negative health impacts (Murray et al., 2019). For example, urban bobcats in southern California that had high anticoagulant rodenticide burdens (Riley et al., 2007) experienced immune dysfunction that explained an increased susceptibility to severe mange (Serieys et al., 2015; Serieys et al., 2018) and contributed to a genetic bottleneck (Serieys et al., 2015). Arsenic is an especially toxic metalloid, ranked first on the 2019 Substance Priority List by the Agency for Toxic Substances and Disease Registry (Agency For Toxic Substances and Disease Registry (ATSDR), 2019). Acute toxicity can result in death, immune dysfunction, or other sublethal effects in wildlife (Sattar et al., 2016; Gupta et al., 2021). Similarly, chromium, usually released into the environment by combustion processes and the metal industry, is one of the most persistent heavy metals,

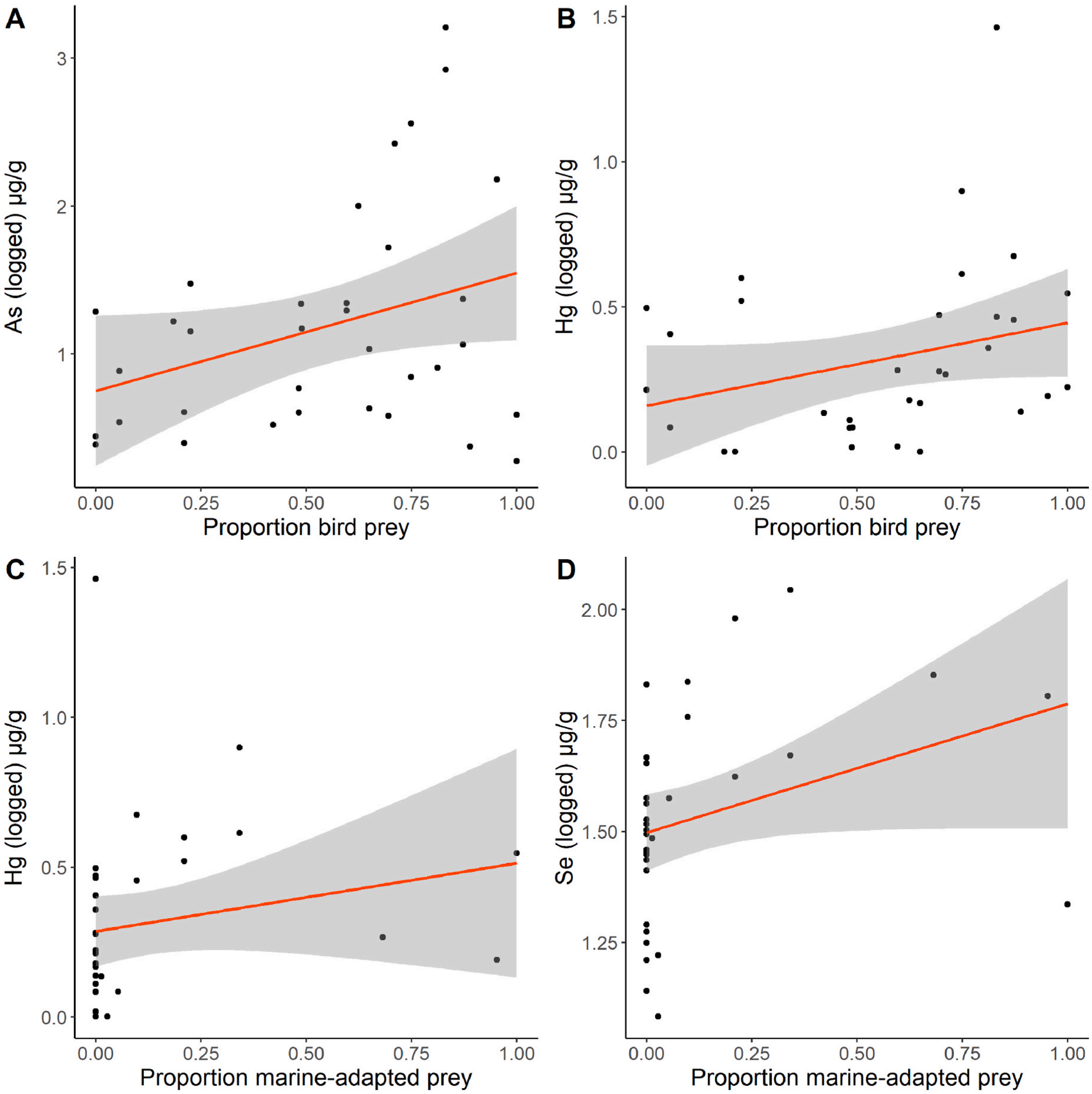

Fig. 4. Associations between metal and metalloid (arsenic, mercury and selenium) concentrations in Cape Town caracal whole blood (n = 34) and (**A – B**) proportion of bird prey (biomass) and (**C – D**) proportion of marine-adapted prey (biomass). Grey area represents 95% confidence intervals.

and is capable of inducing toxicity at low concentrations (Agency For Toxic Substances and Disease Registry, 2019). Mean arsenic concentrations in caracal blood (mean = 3.74 µg/g) were between three and 12 times higher than in other terrestrial carnivores studied to date (see Table S15 for concentrations), notably the Eurasian otter (mean = 0.27 µg/g; *Lutra lutra*; Brand et al., 2020), raccoon (median = 0.22 µg/g; Souza et al., 2013), wolf (*Canis lupus*; mean = 0.85 µg/g) and fox (mean = 1.1 µg/g Squadrone et al., 2022). Caracal chromium concentrations (mean = 0.29 µg/g Table 2; Table S15) were within the range of other carnivores in the Global North (e.g., Arctic fox *Vulpes lagopus*; mean = 1.4 µg/g (Filistowicz et al., 2012) and red fox *Vulpes vulpes* mean = 0.26 µg/g (Filistowicz et al., 2011); refer to Table S15). However, it should be noted that comparison between different tissues is limited (see Table S15). Interestingly, Evans et al. (2021) found that elevated levels of chromium (mean = 3.5 µg/g) in Malay civet (*Viverra tangalunga*) hair samples correlated with several haematological parameters, including reduced mean corpuscular volume (MCV) and mean corpuscular haemoglobin concentration (MCHC), indicating the onset of regenerative anaemia. We found similar physiological signatures, where several elements (mercury, chromium, manganese, and zinc) were associated with decreased MCHC, suggestive of hypochromic anaemia. In the long term, iron deficiency can affect the immune system and increase disease susceptibility (Willi et al., 2022). Similar to previous work on caracal exposure to organochlorines (Leighton et al., 2022), we found that mercury and selenium exposure were associated with elevated levels of platelets and lymphocytes, suggesting an elevated immune response in individuals with metal exposure (Davis et al., 2008). Currently, sensitivity to these elements in caracals is unknown, but some individuals in the study population are likely to be at risk of their established negative health effects.

4.2. *Increased metal exposure through human-associated landscape use*

Urban environments support multiple anthropogenic point sources of pollution, and accordingly, are generally more heavily contaminated than natural ones (Grimm et al., 2008). Caracals using human-transformed landscapes generally had higher burdens of certain metals, although many were marginally significant. Similar patterns of metal and metalloid exposure have been reported in other species utilising human-transformed spaces (e.g., mercury in Bonelli's eagles, *Aquila fasciata,* in southern Portugal, Badry et al., 2019; arsenic, lead and mercury in flying foxes (*Pteropus* spp.) in Australia, Sánchez et al., 2022) and even Cape Town's remaining indigenous forest patches experience contamination from a combination of vehicular traffic emissions and air pollution via the city's urban and industrial activity (Krüger et al., 2019). Use of urban areas was also associated with higher aluminium concentrations, a metallic element which can be acutely toxic and whose main urban sources include emissions from coal combustion, waste incinerators and road vehicles (Alexandrino et al., 2020; Alasfar & Isaifan, 2021). Further, chromium exposure was associated with higher human population density in caracal home ranges, which supports research suggesting that chromium levels in wildlife increased in urban areas through anthropogenic deposition (Orłowski et al., 2014). Another important landscape feature associated with elevated metal exposure levels, particularly lead and cobalt, was road density. Roads are known to accumulate a wide variety of toxic metals, mostly through vehicle exhaust and non-exhaust emissions (i.e., brake pad and tyre wear; Apeagyei et al., 2011; Ferreira et al., 2016). While leaded petrol was banned in South Africa in 2006, lead is not degradable and continues to be recorded in South African ecosystems and people (Naicker et al., 2013; Naidoo et al., 2017).

In our study area, agricultural areas, particularly vineyards, are generally located at the resource-rich interface between urban and natural areas and may therefore attract adaptable carnivores (Bateman and Fleming, 2012; Humphries et al., 2016). Caracals, like other generalists, frequent agricultural areas to exploit often widely available synanthropic prey species (Ramesh et al., 2017; Leighton et al., 2021). Agricultural landscape use is associated with metal exposure in several carnivore species, e.g., golden jackal (cadmium and lead; Markov et al., 2016) and Malay civet (arsenic, lead, chromium and mercury; Evans et al., 2021). Here, we find evidence of elevated arsenic concentrations in caracals associated with vineyard use. Agricultural-related sources of arsenic include arsenic-based pesticides and fertilisers, and contaminated irrigation groundwater (Roychowdhury et al., 2005; Malan et al., 2014). Although some evidence suggests continued use of banned agrochemicals in the GCT (Dalvie & London, 2001), a more likely source may be contaminated groundwater (Irunde et al., 2022). Agricultural activities have been shown to increase natural rates of weathering and mineralisation of arsenic-containing rocks, causing excess quantities of arsenic to enter groundwater supplies (Casentini et al., 2011). Previous studies on this population also report a relationship between vineyard use and increased exposure to anticoagulant rodenticides (Serieys et al., 2019) and organochlorines (Leighton et al., 2022). Together, these findings suggest that using human transformed landscapes, especially those with high road density and vineyards, represent important metal exposure pathways. Collectively, these findings contribute to growing evidence that urban wildlife are disproportionately exposed to harmful chemical pollutants (Riley et al., 2014). Urban planners, viticulturalists, conservation practitioners, and local government need to collaborate on developing robust chemical remediation plans that reduce harmful pollutants generated from these point sources that are undoubtably 'spilling over' into surrounding natural systems.

4.3. Trophic transfer of metals through aquatic food webs

The transfer of aquatic pollutants to terrestrial food webs is an emerging global research focus (Rimmer et al., 2010; Becker et al., 2018; Huang et al., 2018). As a rule, metals may be transferred and circulate through terrestrial food webs when terrestrial species consume metal-contaminated aquatic biota (Cristol et al., 2008). Caracals with home ranges closer to and including coastal areas, and a diet rich in marine-adapted prey, experienced elevated blood levels of mercury, arsenic, and selenium; we also found that caracals consuming wetland-adapted prey were associated with increased copper, manganese, and zinc exposure. Similar patterns have been observed in red foxes in Poland, where foraging in coastal habitats on primarily piscivorous species resulted in higher mercury burdens (Kalisińska et al., 2009). Further, pumas (*Puma concolor*) accumulate high mercury body burdens by preying on mercury-contaminated prey feeding within wetland and coastal food webs (e.g., Roelke et al., 1991; Weiss-Penzias et al., 2019). Aquatic environments bridging the land-ocean continuum (*sensu* Bouwman et al., 2013) are important environmental sinks, accumulating large quantities of pollutants in their sediments (Gani et al., 2021; Tang et al., 2021), where trophic transfer increases these metal concentrations in terrestrial species at higher trophic levels, elevating the relative toxicity and retention time of these substances (Baby et al., 2010). Our dietary results suggest caracals are likely exposed to aquatic metals and metalloids by exploiting contaminated aquatic food webs, most likely via water- and seabird prey. Caracals exploit numerous seabird species, including Cape cormorants and gulls, while a high proportion of wetland-adapted prey species included aquatic birds like Egyptian geese and the African sacred ibis. The Cape cormorant is a piscivore, feeding mostly on pelagic fish (Ryan et al., 2010; Burger & Gochfeld, 2001) which in turn have reportedly high levels of mercury and other metals (Furness & Cooper, 1982; Bosch et al., 2016), and are likely to influence metal burdens of other mammalian predators in our study area, including Cape clawless otters (*Aonyx capensis;* Okes, 2017) and Cape fur seals (*Arctocephalus pusillus;* Stewardson et al., 1999). This may also have important human health implications for local fishing communities and wider seafood consumers (Chen et al., 2008; Bosch et al., 2015; Petrova et al., 2020).

To protect wildlife and humans from potentially toxic metals and metalloids (especially mercury and arsenic) in aquatic environments, it is crucial to understand the environmental sources of the metals. While caracal exposure to some metals may be at the marine interface, the original point sources of mercury and arsenic, for example, may include coal combustion, domestic fuel burning, natural fires and wastewater from cities (Driscoll et al., 2013; Bundschuh et al., 2021). Exposure via these point sources can be directly reflected in wildlife. For example, Bonelli's eagles that were located close to coal-fired power plants had elevated levels of mercury (Badry et al., 2019). In South Africa, coal-fired power plants are major contributors to mercury emissions (approximately 78% of national mercury emissions) at levels well above the global average (Masekoameng et al., 2010). While all coal-power stations in South Africa are located in provinces outside our study area, mercury and arsenic are capable of long-distance atmospheric transport (Marx & McGowan, 2010; Wai et al., 2016). Further, domestic fuel burning for cooking, heating (Buthelezi et al., 2019) and waste disposal (Haywood et al., 2021), especially from informal settlements, is a significant source of local air pollution (Bagula et al., 2021). The limited treatment of wastewater has also resulted in contamination of local aquatic systems and biota (Petrik et al., 2017; Zackon, 2021). Additionally, both natural and human-induced vegetation fires are yearly occurrences in Cape Town and may be sources of atmospheric mercury emissions (Wiedinmyer & Friedli, 2007). The Greater City of Cape Town is a fire-prone and fire-adapted landscape and indigenous vegetation (mainly fynbos) burns periodically in fire cycles of 10–15 years (van Wilgen et al., 2010). For example, Brunke et al. (2001) reported that a large veld fire at Cape Point (a protected, coastal area in the southern section of the study area; Fig. 1) was responsible for releasing large amounts of mercury into the atmosphere, and which was subsequently deposited in the area. Caracals who forage extensively in coastal areas in our study area support elevated mercury concentrations, and fires may contribute to their exposure pathways. Further, anthropogenic activity is increasing the frequency of fire in Cape Town, which will likely increase future mercury release and deposition in the region (Forsyth & van Wilgen, 2008). Although more detailed research is required to better understand the association between mercury accumulation in wildlife due to local vegetation fires, these results suggest a combination of both local and long-distance atmospheric transport of metals likely influences metal exposure in the region's terrestrial wildlife (Treu et al., 2022).

4.4. Does urban landscape use increase the risk of an ecological trap for wildlife?

Urban areas, roads and vineyards may present as attractive foraging areas for certain terrestrial carnivores (Fleming & Bateman, 2018); however, we suggest that by exploiting these areas caracals are exposed to potentially harmful metals and metalloids. Our results point to potentially negative physiological effects of metal exposure, which together with potentially lethal effects of anticoagulant rodenticides (Serieys et al., 2019) and immune impacts of organochlorines (Leighton et al., 2022), reveals a complex system of ecological and fitness trade-offs for the species. Our findings indicate that caracals utilising human-transformed landscapes in our study area (i.e., urban areas, roads and vineyards) are more likely to be exposed to several harmful metals and metalloids, such as aluminium, arsenic, cobalt and lead. Therefore, a possible 'ecotoxicological' trap exists for wildlife foraging at Cape Town's urban edge characterised by exposure to multiple pollutants, including rodenticides (Serieys et al., 2019); organochlorines (Leighton et al., 2022) and toxic metal elements. Ecological traps are fundamentally characterised by negative fitness effects due to suboptimal habitat selection (Schlaepfer et al., 2002). Wildlife faced with high metal burdens reportedly suffer severe health implications, including reduced reproductive success and lower survival rates (Kunito et al., 2008; Tartu et al., 2013). We find that metal exposure was associated with increased measures of anaemia and levels of infection-fighting cells suggestive of potential immune impacts; however, further research is required to fully understand the potential fitness effects associated with metal pollutant exposure in caracals. Although ecological traps are difficult to demonstrate (Robertson & Hutto, 2006), this study contributes to the growing global evidence base suggesting that city margins may exert a 'heavy burden' of toxicants on urban-adapters (Vlaschenko et al., 2019; Zuñiga-Palacios et al., 2021).

5. Conclusions

Our findings suggest that human-transformed areas are important sources of metal and metalloid exposure in Cape Town's caracal population and likely affect the city's wildlife more broadly. This is the first study to report whole blood metal and metalloid concentrations in caracal, and the first for an African terrestrial mammalian carnivore. Overall, our contributes towards a growing global evidence base suggesting that cities may be imperceivably toxic areas for wildlife, especially where there is a high likelihood of co-exposure with other pollutants and pathogens. For the well-being of both humans and wildlife, it is crucial that cities work to reduce the large quantities of chemical pollutants released into their surrounding environment. In Cape Town, this could be focused on the urban edge, waste management, water treatments, roads, and agricultural areas. Mitigation options include bioremediation of contaminated wetlands, stricter regulations on the treatment of city wastewater and the reduction of fuel-burning emissions, monitoring of legal and illegal pesticide use, and reducing road runoff by installing porous pavements (i.e., permeable paving surfaces; Brattebo & Booth, 2003; Schieritz, 2016). These findings support broader research revealing widespread metal contamination in terrestrial and aquatic systems across South Africa (Ansara-Ross et al., 2013; Bosch et al., 2015; Gilbert, 2015). Yet, metals and metalloids are not currently included in South Africa's national air and water quality monitoring programmes (Western Cape Department of Environmental Affairs and Development Planning, 2018). Going forward, and in keeping with the One Health approach (van Helden et al., 2013; Frazzoli et al., 2015), it is crucial that South Africa develops a robust pollutant monitoring programme using a variety of sentinel species; including small and medium-sized carnivores and aquatic bird species. We argue that the caracal is an effective sentinel for metal exposure in human-transformed landscapes (Bateman & Fleming, 2012; Jooste et al., 2014) and will also contribute to broader pan-continental contaminant tracking.

Author contributions

Kim Parker: Conceptualization, Data curation, Formal analysis, Writing – original draft. Jacqueline M. Bishop: Conceptualization, Supervision, Resources, Writing – review & editing. Laurel E.K. Serieys: Conceptualization, Writing – review & editing. Rafael Mateo: Conceptualization, Investigation, Resources, Writing – review & editing. Pablo R. Camarero: Investigation, Methodology. Gabriella R. M. Leighton: Conceptualization, Formal analysis, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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