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Research Article

Urban waste no replacement for natural foods—Marabou storks in Botswana

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Abstract

We compared diets of marabou storks *Leptoptilos crumenifer* foraging from urban landfills and natural areas in northern Botswana using stable isotope analyses and inductively coupled plasma mass spectrometry on moulted feathers. There were significant differences in the diet of marabous foraging from natural areas compared to urban waste sites, reflected by lower δ^{13}C and less enriched δ^{15}N concentrations in those feeding at landfills, suggesting a shift in trophic niche. Feathers from birds foraging at landfills also had significantly higher concentrations of chromium, lead, nickel, and zinc and lower levels of cadmium and potassium than feathers sampled from natural areas. We also analysed marabou regurgitant (42 kg, naturally expelled indigestible food resources) from the Kasane landfill site. More than half was plastic, with single regurgitants weighing up to 125 g. Urban waste stored in open air landfills is altering some marabou diets, affecting their natural trophic niche, resulting in the consumption (and regurgitation) of large amounts of plastic, and exposing marabou to potentially chronic levels of trace metals. Despite the marabou's apparent resilience to this behavioural shift, it could have long-term effects on the population of the marabou stork, particularly considering Botswana has some of the few regular marabou breeding colonies in southern Africa.

Key words: ICP-MS, stable isotope analysis, waterbird, Africa, refuse, garbage

Introduction

As human populations increase and concentrate in the world's cities (Kowarik 2011; Giles-Corti et al. 2016; Zhang 2016), direct and indirect interactions with wildlife also increase. Urbanisation effects such as habitat loss and degradation, pollution, disease (Duh et al. 2008; Laurance 2010; Crist et al. 2017), and human–wildlife conflict (Thirgood et al. 2005; Dickman 2009; Lamarque et al. 2009; Dunham et al. 2010) are the cause of much of these interactions, which commonly arise between people and bird species (Mateo-Tomás et al. 2012, Redpath et al. 2013; Lambertucci et al. 2015; Oduntan et al. 2015; O'Bryan et al. 2018). Such interactions occur globally, including within urbanising populations of African countries (Thabethe and Downs 2018).

In low- and middle-income countries, waste stored in open air landfills is increasing (Yang et al. 2018), attracting many avian species to the abundant food scraps (Ciach and Kruszyk 2010; de la Casa-Resino et al. 2014). For example, different stork species feed in landfill sites across Europe, Africa and America (Ciach and Kruszyk 2010), altering their diet. The ingestion of waste, including plastic and trace metals, as a result of this dietary shift can result in mortality from poisoning (Piper 2004), decreased egg production and increased hatchling mortality (Malik and Zeb 2009; Lavers et al. 2014; Abdullah et al. 2015; Liu et al. 2019).

The marabou stork *Leptoptilos crumenifer* has frequented human landfill sites for more than six decades (Kahl 1966). They are widely distributed across Africa (Brown et al. 1982), naturally feeding on insects, fish, frogs, small mammals, small reptiles, including young crocodiles, birds and carrion (Maclean et al. 1993). They can swallow large whole food items, weighing up to 600 g (Hancock et al. 2010), which they process in their crop, regurgitating unwanted parts (e.g. bone). When feeding at landfill sites, they use this behaviour to regurgitate unwanted plastic, foil, cardboard, polystyrene and even a knife (Hancock et al. 2010). Little is known about the effect of this novel feeding behaviour on individuals or populations, although marabou chicks had slow development near a Kenyan landfill site (Kahl 1966).

Due to the use of regular roosting sites (Pomeroy 1973), the collection of discarded marabou feathers is a simple and non-invasive sampling method. Feathers can provide a dietary signature, reflecting both trophic level and dietary niche information, and trace metal uptake (Furness et al. 1986; Mizutani et al. 1992; Markowski et al. 2013). Niche and trophic level changes can be detected with isotopic analyses, as the isotopic composition of an animal's tissues reflect its diet (DeNiro and Epstein 1978, 1981). In feathers in particular, the isotopic composition reflects diet during feather growth (Hobson and Clark 1992; Dauwe et al. 2003), with nitrogen isotope ratios undergoing a stepwise enrichment with trophic level (DeNiro and Epstein 1981), and carbon ratios indicating dietary contributions from differing sources (e.g. freshwater vs. terrestrial plants) (DeNiro and Epstein 1978). A changing dietary niche in a top predator and scavenger such as the marabou stork could have cascading effects through the ecosystem (Reznick et al. 2008; Letnic et al. 2009; Antiqueira et al. 2018), opening the niche to other (often invasive) species (González-Moreno et al. 2015) and affecting interspecies resource partitioning and competition (Córdova-Tapia et al. 2015; Wang et al. 2018). Trace metals ingested in dietary items can be detected in feathers, given that metals absorbed through the intestinal tract can be sequestered in feathers (Furness et al. 1986) during feather growth. Therefore, comparison of isotopic ratios and metals in feathers can help differentiate variations in the diets among and within bird populations, reflecting site specific feeding responses (Doucette et al. 2011; Jackson et al. 2011; Hebert et al. 2016; Mikoni et al. 2017).

Marabou can be frequently seen feeding at landfills in Botswana and to explore the effects of this behaviour we compared isotopic ratios (^{13}C and^{15}N) and trace metal concentrations (Al, Cd, Cr, Cu, Fe, K, Ni, Mn, Pb and Zn) in feathers collected from a range of urban landfills and natural environments. We predicted that the populations feeding at landfill sites would show a shift in their trophic position and feeding niche, reflected by higher ^{13}C and enriched ^{15}N, due to the abundance and variety of terrestrial protein and plant sources available. We also predicted trace metal concentrations in feathers would reflect proximity to landfill sites due to increased likelihood of uptake of metals with ingestion of waste as has been seen in other bird species (de la Casa-Resino et al. 2014). This dietary shift could have serious consequences on individuals, including mortality (Piper 2004), affecting Marabou populations in southern Africa.

Methods

Study area

We studied marabou populations from eight locations across northern Botswana, comprising urban and natural feeders. Marabou fed at two landfill sites: Maun and Kasane. Maun and Kasane landfill sites contained household, hospital, industrial and mechanical waste, with abattoir waste also present at the Maun landfill. Adjacent to the Kasane landfill (~500 m), there was a fenced reserve where marabou roosted nightly, returning daily to feed at the landfill. These three locations comprised the urban feeding marabou populations of our study. Naturally feeding marabou populations also occurred at three locations within Chobe National Park, about 50km from the nearest landfill [between Ngoma (C3) and Ihaha Campsite (C1), Fig. 1], and from two sites within the Okavango Delta, about 80 km from the nearest landfill [Chiefs Island (CI) and Kanana breeding colony (KC), Fig. 1].

Sampling

We collected 60 discarded feathers from across the eight locations that were cleaned on site with filtered water, and then dried and packaged for later stable isotope and trace metal analyses.

We also collected regurgitate (once every 2 weeks, 18 June 2018 to 25 August 2018) from marabou at the site adjacent to the Kasane landfill (KR, Fig. 1), where they habitually regurgitated. Regurgitate was sun-dried, weighed and sorted by material, colour, size and brand. We also compared this collection of materials, colours, sizes and brands of major rubbish types with four randomly selected and photographed areas (2 m × 2 m) of the Kasane landfill site (21 September 2018).

Stable isotope and trace metal Inductively coupled plasma mass spectrometry (ICP-MS) analyses

We removed any remaining surface dirt on feathers with distilled water, followed by vigorous washing in deionized water (RO) and a chloroform methanol solution wash [see Methods in Paritte and Kelly (2009)] to remove any surface oils. Feathers were then left to air dry for 24–48 hours. Feathers were identified as either body or flight feathers based on their size, colouration and structure. For stable isotope analyses, feather barbs from the tip of each feather were clipped, placed in tin capsules and weighed (~500 μg). Standards of glutamic acid 40 and glutamic acid 41 were analysed at the beginning, middle and end of each run through the mass spectrometer (Seminoff et al.

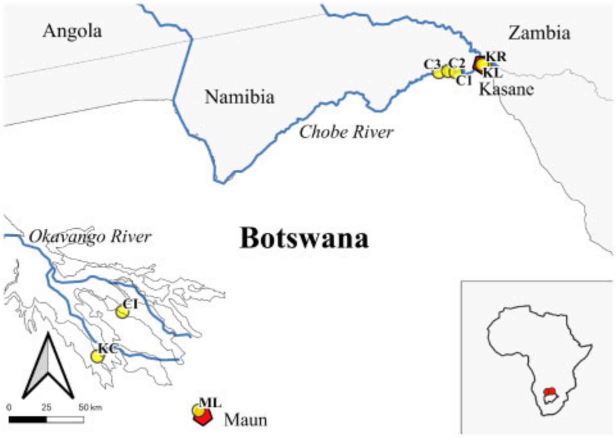

Figure 1: Eight locations across Botswana (yellow circles) where feathers of marabou storks were collected from five natural environments, including the Okavango Delta [Kanana Colony (KC, n = 9, 22.8582,−19.5429) and Chiefs Island (CI, n = 10, 23.0064, −19.2746)] and Chobe National Park [C1 (n = 5, 25.0156,−17.8313), C2 (n = 3, 24.9666, −17.8249) and C3 (n = 1, 24.9113, −17.8331)] and two landfill sites [red pentagons, Maun Landfill (ML, n = 10, 23.4657, −19.8688) and Kasane landfill (KL, n = 2, 25.1706, −17.7869), which also included the adjacent Kasane Reserve (KR, n = 20, 25.1884, -17.7853)] at the respective urban communities of Maun and Kasane.

2007), with their accuracy measured as continuous flow isotope ratio mass spectrometry for $\delta^{15}N$ and $\delta^{13}C$ values (Brenna et al. 1997). For ICP-MS analyses of trace metals (aluminium, cadmium, chromium, copper, iron, lead, manganese, nickel, potassium and zinc), a piece ~4 × 2 cm of feather was removed from the top of the vane of each feather, avoiding the centre rachis, sampling about 0.2 g (DeNiro and Epstein 1981). Samples were digested with HNO_3 (open), and then analysed using an inductively coupled plasma mass spectrometer (ICP-MS, Perkin Elmer, NexION 300D with universal cell technology). Calibration standards were prepared from commercial stock standard solutions, referenced to certified bovine liver (Altmeyer et al. 1991; Kim et al. 1998; Cardiel et al. 2011) (Supplementary Table S1).

Statistical analyses

We separately modelled for differences in $\delta^{13}C$ and $\delta^{15}N$ ratios across sites, varying in distance from the closest landfill (Fig. 1). We used a linear modelling approach, with the glmmTMB package (Brooks et al. 2017), with fixed predictor variables including collection site (converted to a numerical variable based on the distance from the closest landfill); collection region (Chobe in the East vs the Okavango in the West) and feather type (body vs flight). We included region in the model to account for geological differences, which may alter trace metal concentrations naturally present in the environment (Huntsman-Mapila et al. 2005; Kelepile et al. 2020). We performed a power analysis on the $\delta^{13}C$ and $\delta^{15}N$ model results using the pwr package (Champely et al. 2018), with both falling above the standard 0.8 threshold indicating our significance testing was valid (Cohen 1965).

To determine differences in the isotopic niches of the marabou population, we then divided the feathers into three distance divisions: 1) marabou feeding at the landfills in Maun and Kasane (<10 km), 2) in Chobe National Park, where they potentially still visit the Kasane landfill (10–55 km) and 3) those unlikely to be frequently visiting landfills in the Okavango Delta (>55 km). We used the R package SIBER (Jackson et al. 2011) to visualise the standard ellipse areas representing niche widths and fitted Bayesian models to the data, using the rjags package (Plummer 2013). We also calculated the overlap of the niche area occupied by each group using the package nicheROVER (Lysy et al. 2014), with the Monte Carlo method to bootstrap the same number of samples for each group (500), repeated 500 times ($\alpha = 0.05$), averaged to provide final percentages.

To model trace metal concentrations in feathers, we used separate glmmTMB models (with a gaussian family), including collection region, distance from landfill sites and feather type as predictor variables. No trace metals fell below the measurement detection limit, and so all were included in the modelling (Supplementary Table 1). We used the DHARMa package (Hartig 2020) to visualise the QQplot and the residual vs predicted values of all glmmTMB models, checking the data satisfied the assumptions of normality and homogeneity of variance. We log transformed Al, Cr, Cu, Fe, K, Ni and Pb concentrations because data were skewed. Finally, we compared trace metal concentrations with suggested avian healthy limits (Malik and Zeb 2009; Ullah et al. 2014; Abdullah et al. 2015).

Results

Regurgitate

We collected 42.18 kg of regurgitant from six ranked rubbish groups: paper and cardboard, soft plastics, bone, aluminium foil, miscellaneous and polystyrene (Table 1, Fig. 2). Some single regurgitants weighed up to 125 g, with single boluses of plastic weighing up to 83 g, or paper up to 43 g (Fig. 2). Ninety-five percent of all soft plastic collected was thin and clear, resembling cling-wrap with minimal coloured plastics. As well, we identified 110 individual items (Supplementary Table S2), in seven major groupings (Table 2). While we could not quantify the total amount of rubbish regurgitated fortnightly in our study area (due to its multiple uses and the presence of dangerous animals), the regurgitant was continually deposited, with fresh wet regurgitants present each time the site was visited (Fig. 2). In comparison, rubbish at the Kasane landfill consisted of hard plastic soft drink bottles, plastic bags of all colours and a large amount of cardboard and paper (Table 1, Supplementary Table S2).

Stable isotope analyses

There was considerable variation in feather $\delta^{13}C$ and $\delta^{15}N$ concentrations in relation to location (n = 59, Table 3). Feather type was not a significant predictor of $\delta^{13}C$ ($\chi^2(1, N=59) = 0.03$, $P=0.84$) or $\delta^{15}N$ ($\chi^2(1, N=58) = 0.00$, $P=0.98$). Region was not a significant predictor of $\delta^{13}C$ ($\chi^2(1, N=59) = 0.31$, $P=0.57$); however, it was a significant predictor of $\delta^{15}N$ ($\chi^2(1, N=58) = 7.87$, $P=0.005$), more enriched in the Okavango Region than the Chobe Region.

Concentrations of $\delta^{13}C$ in feathers were significantly less depleted, with distance from the closest landfill ($\chi^2(1, N=59) = 7.04$, $P=0.008$, Fig. 3). Similarly, concentrations of $\delta^{15}N$ in feathers were significantly more enriched with distance from the closest landfill ($\chi^2(1, N=58) = 22.31$, $P<0.001$, Fig. 3). Differences among feeding preferences were reflected in the niche width of the groups (Fig. 4), with the largest ellipses in the mid-distance group (10.32, 10–55 km), indicating a more varied diet in both $\delta^{13}C$ and $\delta^{15}N$ sources. Ellipse size was followed by the furthest distance group (9.95, >55 km), and finally the group closest to a

Table 1: Relative components of rubbish collected from marabou regurgitations from the Kasane Reserve (18 June 2018 to 25 August 2018, Fig. 1) and major rubbish components within the Kasane landfill

Material	Example	Regurgitant (kg)	Regurgitant (%)	Landfill (%)
Paper and cardboard	Butter wrapper	10.64	25.23	40
Soft plastics	Cling wrap	22.88	54.25	30
Hard plastics	Plastic bottle tops	0.00	0	20
Foil	Individually wrapped ice cream	0.72	1.7	<5.00
Bone	Beef bone	7.77	18.42	<1.00
Polystyrene	Take away food containers	0.03	0.06	<5.00
Miscellaneous	String	0.05	0.11	10

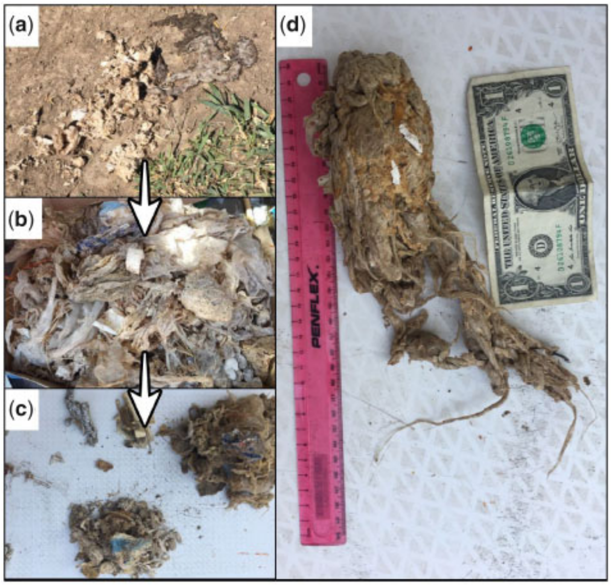

Figure 2: Marabou regurgitate was collected from the reserve neighbouring the Kasane landfill site (18 June 2018 to 25 August 2018), with continual fresh depositions of regurgitate during the collection period (a). Regurgitate was collected, compiled (b) and sorted into plastics, paper, bone, aluminium foil and miscellaneous (c). Some regurgitants consisted of many small pieces (a), whilst some were large single boluses (d). A single bolus is displayed next to a United States of America dollar bill for size reference.

Table 2: Items within the Marabou regurgitate that were able to be identified sorted into their major groupings by type and summarised by the number of occurrences in the total 42kg of collected marabou regurgitant collected from the Kasane Reserve (18 June 2018 to 25 August 2018, Fig. 1)

Regurgitant by type	Example	Occurrences (n)	Occurrences (%)
Dairy	Butter, ice cream, cheese, milk powder	22	20.00
Deli	Food bags, polystyrene food containers, take away containers	7	6.36
Meat	Processed chicken, ham, sausage, salami, devon, polony	48	43.64
Miscellaneous	Spaghetti, string, sock, twine, stockings	8	7.27
Snack food	Chips, biscuits, coffee, soft drink, lollies	13	11.82
Sanitary items	Toilet paper, face mask, bandage, make up wipes, wet wipes	9	8.18
Soap	Soap and body wash	3	2.73

landfill site (8.33, <10 km; Table 3, Fig. 4), indicating the landfill feeders had a smaller range of dietary sources contributing to the δ^{13}C and δ^{15}N ratios in their feathers. Credible confidence intervals of niche width were the largest in the mid-distance group, indicative of considerable individual variation in diet (Supplementary Table S3). There was therefore considerable separation amongst feeding groups, with a 74% probability of natural feeders (furthest distance group) feeding within the mixed group's niche (mid-distance), compared to a 50% probability of natural feeders feeding within the landfill niche. Landfill feeders showed an 83% probability of feeding within the niche of the mixed group, but only a 48% chance of niche overlap with the natural feeders. The mixed feeders were more likely to be feeding within the landfill niche (77%) than the natural niche (73%).

Table 3: Mean (±SD, n) concentrations for δ^{13}C and δ^{15}N analysed in feathers (59) collected across different sites (Fig. 1) and their distances from the landfill sites in parentheses with the three SIBER groupings used to explore dietary niche, varying with distance in northern Botswana

Distance from landfill (km)	δ^{13}C	δ^{15}N
Kasane Landfill (0)	−17.72 (±1.81, 2)	9.78 (±0.86, 2)
Maun Landfill (0)	−20.15 (±3.05, 10)	10.24 (±1.15, 10)
Kasane Reserve (0.5)	−19.26 (±2.6, 20)	9.23 (±0.71, 20)
Chobe National Park C1 (49)	−19.72 (±0.88, 6)	10.04 (±1.08, 6)
Chobe National Park C2 (51)	−17.19 (±4.75, 3)	10.42 (±1.57, 3)
Chobe National Park C3 (53)	−17.88 (1)	12.18 (1)
Kanana Colony (78)	−19.77 (±3.27, 7)	11 (±1.02, 7)
Chiefs Island (88)	−15.68 (±1.23, 10)	12.07 (±0.73, 10)
SIBER Landfill Feeders (<10)	−19.44 (±2.71, 32)	9.58 (±0.97, 32)
SIBER Mixed Feeders (10–55)	−18.78 (±2.64, 10)	10.37 (±1.28, 10)
SIBER Natural Feeders (>55)	−17.36 (±3.02, 17)	11.63 (±0.99, 17)

Trace metal analyses

There were significantly higher concentrations of aluminium, chromium, iron, potassium, manganese, nickel, lead and zinc in flight feathers compared to body feathers ($n = 60$) (Supplementary TablesS4 and S5). Copper was the only metal with significantly higher concentrations in body feathers (Supplementary Table S4 and S5). Metal concentrations of aluminium, chromium, lead and zinc also decreased with distance from the closest landfill, while potassium and cadmium increased with distance from the landfill site (Supplementary Table S5, Fig. 5). Although iron and manganese concentrations did not differ with distance to the landfills, they were potentially approaching toxic concentrations. These high concentrations were particularly apparent in the Chobe Region, with the highest mean concentrations in feathers collected from the Kasane landfill (Supplementary Table S5). Cadmium, copper, iron and nickel concentrations in the feathers were significantly higher in the Chobe Region, whilst lead and potassium were higher in the Okavango Delta Region (Supplementary Table S6).

Discussion

The interactions between urban waste and wildlife are increasing globally, including within many African countries (Cobbinah et al. 2015). Marabou storks exemplify this challenge around landfill sites in northern Botswana. The constant deposition of marabou regurgitant collected in the Kasane Reserve is indicative of this shift in feeding preferences, confirmed by depleted δ^{13}C and δ^{15}N and reduced feeding niches for those feeding at landfills. Furthermore, individuals feeding at the landfill sites showed significant differences in the trace metal composition of their feathers, with Fe and Mn approaching or exceeding possibly lethal limits.

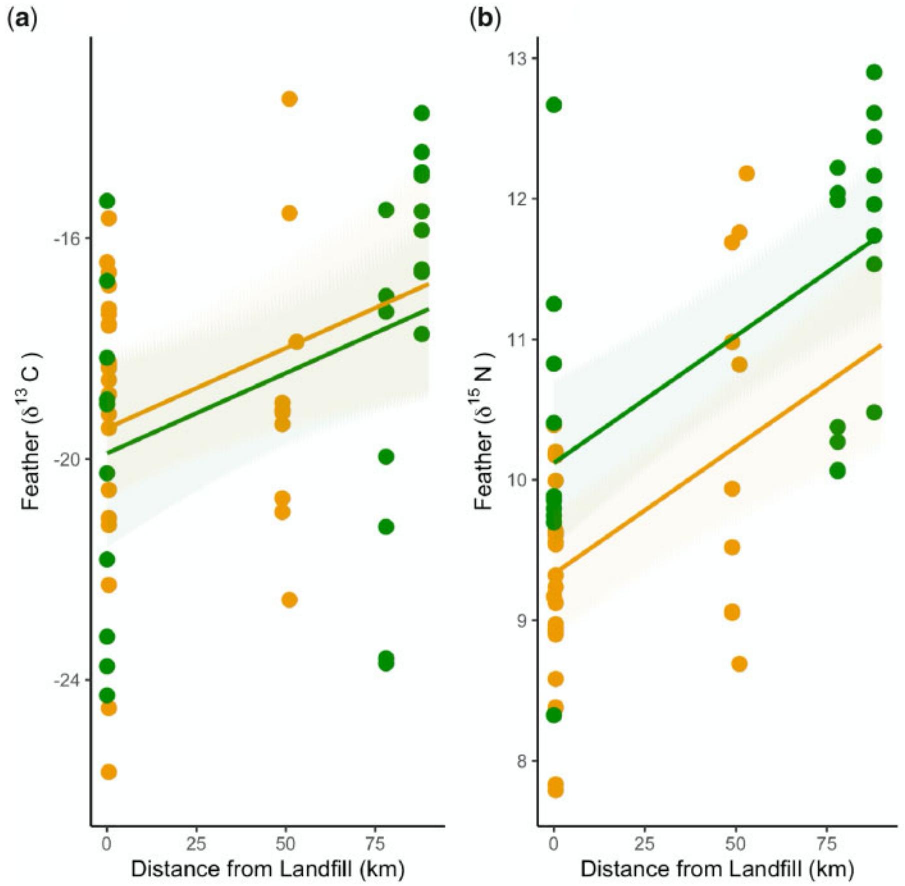

Figure 3: Predicted responses of δ^{13}C (a) and δ^{15}N (b) ratios to distance from the closest landfill site in feathers (n = 59) collected from eight locations across northern Botswana in the eastern Chobe region (orange) and the western Okavango region (green) (Fig. 1), with model 95% confidence interval (coloured bands).

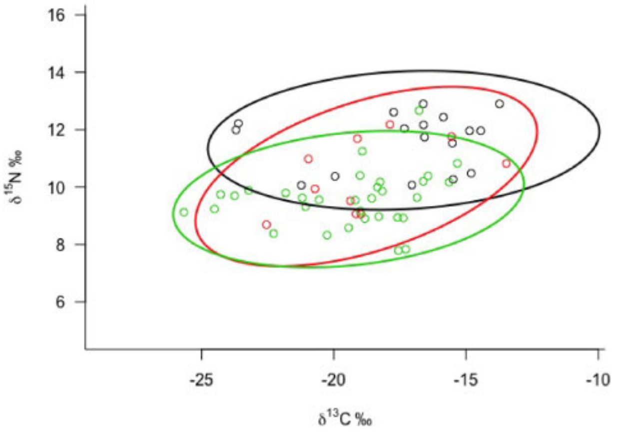

Figure 4: Trophic niches developed from δ^{13}C and δ^{15}N ratios for marabou feathers (n = 59) collected at differing distances from landfills across northern Botswana; <10 km (green), 10–55 km (red) and >55 km (black), expressed as corrected standard ellipses.

The remarkable ability of the marabou to regurgitate large chunks of indigestible material (Fig. 2) is largely ignored both in scientific literature and general information, with only one reference from 1988 (Hancock et al. 2010). Our collection of regurgitant indicated marabous was largely consuming high fat, high protein content foods such as meat and dairy at landfill sites (Table 2). Given the range of items at the landfill, and difficulty in finding high protein high fat content foods, marabous clearly selectively sorted through the waste, but still consumed considerable quantities of plastic (Table 1). In particular, large amounts of cling wrap were present in the regurgitate, likely due to considerable wrapping of pre-prepared meals in local grocers (R. Francis, pers. observation), which the marabou then target for their food content. Plastic consumption is often lethal for many species of birds, particularly freshwater (Wiemeyer et al. 2017; Battisti et al. 2019) and marine birds (Tanaka et al. 2013; Verlis et al. 2013; Lavers et al. 2014; Wilcox et al. 2015; Roman et al. 2016); however, we only saw two marabou corpses (at the Maun landfill) during this study and so their ability to regurgitate may prevent mortality.

Their altered diet at landfill sites resulted in measurable changes in the δ^{13}C and δ^{15}N in feathers. The depleted δ^{13}C in feathers from landfills (Fig. 3) may represent a shift in the types of plant material being consumed, which at landfill sites may comprise of both aquatic and terrestrial C3 plants (including wheat that was found in the form of spaghetti in the regurgitate), C4 plants, and also paper and cardboard. In contrast, marabou feeding in natural areas likely feed on mainly aquatic and C4 plants that have higher δ^{13}C values, reflected in the slight increase in the δ^{13}C (Deines 1980; Cerling et al. 1997). In contrast to our initial predictions, urban landfill feeding populations showed depleted δ^{15}N (Fig. 3), which may reflect consumption of lower trophic level animal sources, such as herbivores (e.g. meat from cattle), rather than their natural diet of high trophic level organisms.

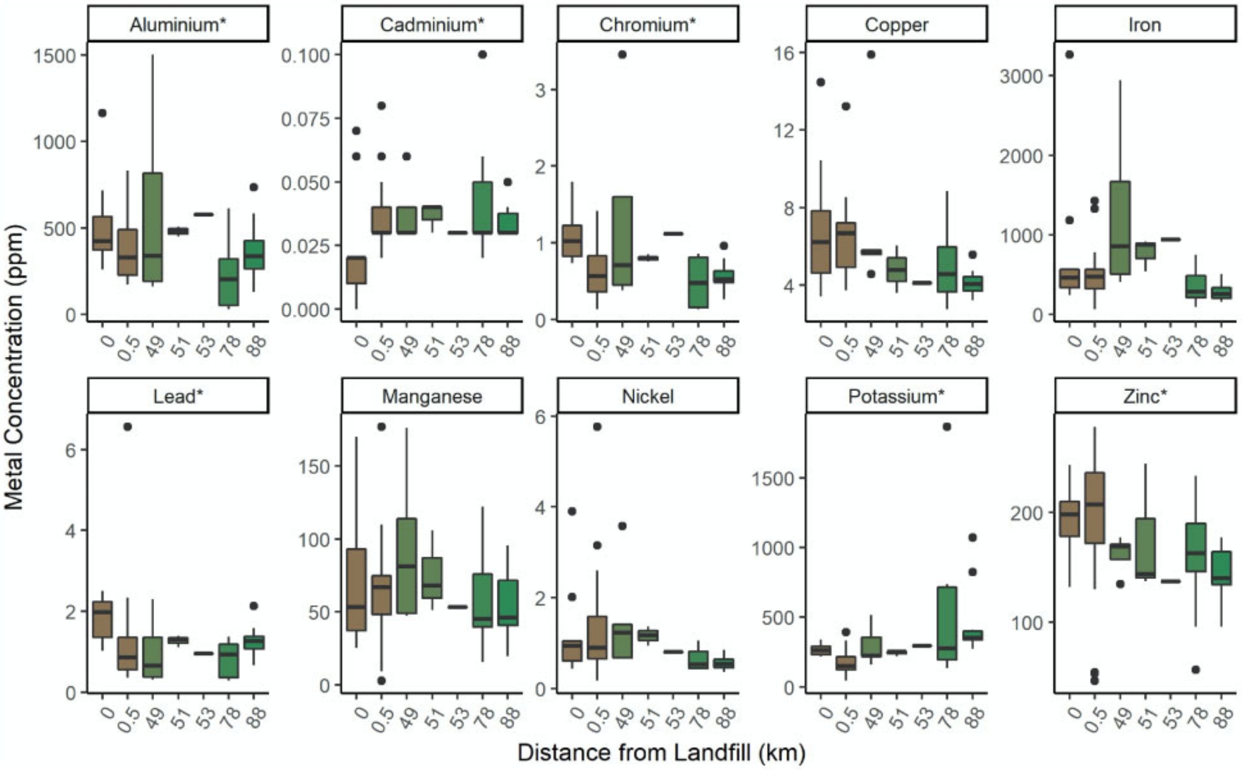

Figure 5: Boxplots of trace metal concentrations following ICP-MS analyses showing significant relationships (*) to distance to the nearest landfill in feathers (n = 60) from eight locations across northern Botswana.

Resultingly, the trophic niche of marabous has narrowed with proximity to landfills sites, a typical niche response where food resources are abundant (Wang et al. 2018). The high overlap of the mid-distance group (10–55 km) with both the natural and landfill feeders was confirmation that this group were mixed feeders, and indicates they may fly up to 55 km to feed at landfill sites. Such foraging information could not be found in published literature for the marabou stork, however the white stork *Ciconia ciconia*, can fly up to 48.2 km to reach landfill sites (Gilbert et al. 2016). The smallest trophic niche overlap occurred between birds feeding furthest from and those closest to landfill sites. The decrease in δ^{15}N of more than 3‰ (one approximate trophic level) between these two groups indicates a small shift in the natural niche filled by the marabou (McCutchan Jr et al. 2003), which as a scavenger and predator could affect herbivore and mesopredator populations, and increase disease in the environment (O'Bryan et al. 2018).

Higher trace metals (aluminium, chromium, lead and zinc) in feathers of marabous feeding at landfill compared to natural sites, probably indicated ingestion of by-products of batteries, paint, mechanical waste, sewerage and the abundant use of aluminium in human products such as anti-perspirant (Kgosiesele and Zhaohui 2010; Ullah et al. 2014). Maximum concentration of chromium and lead surpassed the recommended threshold in only one feather (2.8 and 4 ppm) and so it is unlikely that these trace metals are seriously affecting marabou health (Gochfeld 2000; Burger and Gochfeld 2001). Conversely, potassium levels were relatively low and are essential for growth and heart rhythms, with imbalances attributed to the death of broiler chickens (Hopkinson 1991). Cadmium (a non-essential trace metal) in feathers was highest closest to natural sites, which may be due to its use in phosphate based fertilisers in agricultural areas (Ali and Khan 2018), away from urban centres.

Iron and manganese were at surprisingly high levels in marabou feathers from Chobe National Park, which is of concern, given they can cause fatal iron storage disease, anaemia, micromelia, limb twisting, haemorrhage, stunted growth and behavioural disorders (Sheppard and Dierenfeld 2002). Iron and manganese can originate from uncontrolled waste disposal from the mechanical industry, vehicles, construction materials, diesel fuel burning, untreated traffic waste, industrial effluents and batteries (Kgosiesele and Zhaohui 2010; Ullah et al. 2014). Historically manganese was mined in south western Botswana, beginning in 1957, with mines contaminated and abandoned reducing vegetation cover (Ekosse and Fouche 2005; Ekosse et al. 2006; Abdullah et al. 2015). In 1997, about 15% of ostrich chicks from a farm in Botswana hatched with limb deformities and elevated serum manganese and zinc levels (Mushi et al. 1999). Manganese mining will likely restart in Botswana (Mining Review Africa 2018), potentially posing an ongoing risk to the wildlife of Botswana.

Trace metal concentrations varied between body and flight feathers, found to also occur in other birds (Pon et al. 2011). Higher metal concentrations in flight feathers, compared to body feathers, may relate to longer durations for flight feather growth and therefore a greater uptake of metals into the feathers from blood (Dauwe et al. 2003). While feathers remain a useful tool for the non-invasive analysis of such trace metals, there was limited information on toxicity levels in feathers, and how these concentrations directly related to blood concentrations. Further, considering the large size of the marabou it is possible toxicity levels differ for this species. Necropsies on the corpses at Maun Landfill and blood collection alongside feather collection would provide insight into such uncertainty, as would further studies into potential differences in behaviour and reproduction of affected individuals. Nonetheless there was a clear relationship between feeding on waste, a shift in trophic niche size and trace metal consumption with proximity to landfill sites.

Other species feed at landfill sites in Botswana: African sacred ibis *Threskiornis aethiopicus*, pied crow *Corvus albus*, banded mongoose *Mungos mungo*, warthog *Phacochoerus africana*, hyena *Crocuta crocuta* and baboon *Papio ursines* (R. Francis, personal observation). Banded mongoose feeding at the landfill site in the Chobe Region of Botswana carry more disease pathogens and are more aggressive than other populations (Flint et al. 2016), and a Ugandan population feeding at urban refuse sites had higher body condition but higher mortality rates in young males than other populations in natural settings (Otali and Gilchrist 2004). Many baboons died from an outbreak of bovine tuberculosis from meat in a Kenyan landfill site, changing the culture of the troop for decades (Sapolsky and Share 2004). Hyenas change their behaviour around landfill sites, potentially increasing predation risk to urban livestock (Kolowski and Holekamp 2008), including donkeys (Yirga et al. 2012). Urban communities are also affected by the spreading of waste (e.g. sanitary items, Supplementary Table S2), potentially carrying disease outside landfill sites (Cook et al. 2008).

Rubbish at landfill sites is generally buried or covered in Botswana (Suresh and Vijayakumar 2012), ideally preventing animals feeding, but this is not routine at the Kasane site. Regular burying could reduce marabou and other wildlife foraging at this landfill site. There are other remedial measures available, including exclusion of wildlife from landfill sites through fencing or netting (Flint et al. 2016); however, this is difficult, dangerous to the animals and expensive (Conover 2001). Recycling also reduces landfill rubbish, a practice increasing in Botswana (Mmereki 2018), as does reduction of food waste (Newsome and van Eeden 2017).

Considering the few corpses, wide distribution (Brown et al. 1982), and abundance of marabou storks, it is unlikely this behaviour is causing high mortalities despite decades of feeding at landfill sites (Hancock et al. 2010), but deserves further investigation. Some populations of the marabou may be higher in urban than natural areas (Pomeroy and Kibuule 2017), and landfill sites and urban areas provide food for some animals when there is low natural availability (Plaza and Lambertucci 2017), including other avian species (Meyer-Gleaves and Jones 2007; Tauler-Ametller et al. 2018). The marabou stork, therefore, is possibly one of the few species better suited to exploiting this resource, although not totally without consequence.

Landfill sites around urban communities alter the diet of the marabou, changing its natural trophic niche, causing the swallowing and regurgitation of large amounts of waste and exposing the species to trace metal toxicities. The marabou's ability to regurgitate indigestible material probably reduces the effects of rubbish ingestion, but not completely. This is a burgeoning issue as African countries urbanise (Cobbinah et al. 2015), and one requiring close monitoring. There is a need to improve recycling and reduce and remove human waste to address this impact, considering both the role of landfills in providing a consistent food source to the resilient marabou, but also potentially affecting the health and behaviours of other less resilient species.

Conclusions

The marabou stork has fed at landfill sites for decades, and despite this behaviour is an abundant and widely distributed species. As Africa increasingly urbanises, more waste will likely be stored in open-air landfills and the costs to marabou storks shifting their feeding from natural to urban areas may also increase. The swallowing and regurgitation of large amounts of plastic and human waste, the alteration of the marabou's natural trophic niche, and the increased exposure to toxic trace metals may affect the future conservation of this species, as for other species which regularly visit landfill sites. Alternatively, like some avian species marabou may continue to benefit from urbanisation and landfills, becoming a success story despite increasing natural habitat loss. We need to understand more about the lethal and sublethal effects of feeding at landfill and the implications for reproductive success to ensure southern African populations of urban marabou persist.

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Supplementary data

Supplementary data are available at *JUECOL* online.

Statement of data availability

Raw data is provided on Dryad DOI https://doi.org/10.5061/dryad.pg4f4qrm2.

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