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Possible factors affecting the bioavailability of copper and the copper requirements of wild, free-ranging African herbivores: A review

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Abstract

Free-ranging wild herbivores in Africa comprise 78 species of ruminants and several species of monogastric hindgut fermenters, and are classified as grazers, mixed feeders, and browsers. The objective of this review is to provide guidance to wildlife nutrition advisers by outlining key metabolic principles relevant to assessing copper nutrition in herbivores. In domestic species, copper bioavailability is influenced by dietary copper antagonists, copper solubility at absorption sites, and the homeostatic regulation of copper metabolism. Differences in the homeostatic control of copper absorption and metabolism in the liver between ruminants and monogastric species have a major effect on their tolerance to excessive copper exposure. As some elements in the diet are antagonistic to copper solubility in the digestive tract, dietary copper concentration alone has limited diagnostic value for assessing the potential copper nutrition status of a ruminant. Dietary copper is most soluble in acidic environments and factors influencing rumen pH, such as the effect of diet type on rumination and saliva flow, could thus influence copper solubility. In monogastric species, the solubility of dietary copper in the stomach can be high (up to 80% *in vitro*) because of the acidic environment of the stomach. Consequently, in domestic species, the bioavailability of copper varies from 1% to 10% in mature ruminants, compared with an estimated ≥30% for non-ruminants. This suggests that for wild species with similar body weights and diets, dietary copper requirements per kilogram of feed intake for maintenance should be substantially lower for monogastric species than for ruminants.

Keywords: antelope, bioaccessibility, hindgut fermenters, ruminants, trace elements, wildlife

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Introduction

In Africa, herbivorous game animals comprise 76 bovid ruminant species (Gagnon & Chew, 2000), two species of Giraffidae, and several non-ruminant hindgut fermenters. Because these species are free-ranging, evaluating their trace element nutrition poses a significant challenge for animal nutritionists and advisers. A substantial amount of research has been conducted on various aspects of digestive physiology in captive wild animals, including on aspects of trace element metabolism

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(Dierenfeld, 1997), and this remains an active field of study. In contrast, direct data on free-ranging wildlife are scarce, making it difficult for advisers to assess factors such as the quantity and quality of forage consumed and the bioavailability of trace elements. This review explores how dietary strategies and digestive morphophysiology influence copper bioavailability in herbivores, with particular emphasis on free-ranging African wildlife. Current understanding is largely derived from research on captive animals and domestic herbivores with similar feeding strategies. Although precise trace element intake cannot be determined in free-ranging species, identifying the factors that regulate copper bioavailability provides a useful framework for evaluating nutritional status. The aim of this review is to assist animal nutritionists and wildlife managers in assessing the copper status of game species under extensive, low-input management systems. As no comparable review on the issues covered has been published, it addresses an important gap in the literature.

Understanding the bioavailability and utilisation of copper in free-ranging herbivores requires classifying species according to their anatomical characteristics, digestive physiology, and dietary adaptation. Ruminants (foregut fermenters) are categorised according to their feeding strategy into grazers (obligate or variable), mixed feeders (intermediate or generalist), browsers, and frugivores. Diet selection within these groups is influenced by forage quality, with larger species generally consuming more fibrous diets than smaller ones (Owen-Smith, 1999; Clauss *et al.*, 2010). Non-ruminant hindgut fermenters comprise colon fermenters (such as elephants, rhinoceroses, and equids) and caecum fermenters (including warthogs, rabbits, and hares), with at least some of the caecum fermenters practicing coprophagy (Dehority, 2002). The hindgut fermenters can also be classified by feeding strategy, being described as grazers (e.g. white rhinoceros, zebras), mixed feeders (e.g. elephants, with a browsing tendency), and browsers (e.g. black rhinoceros) (Sahu & Kamra, 2002; Hummel *et al.*, 2020). Hippopotami represent a unique case, as they are non-ruminating foregut fermenters; however, little is known about their copper metabolism and no comparable domestic model exists (Nakayama *et al.*, 2012), and it therefore remains unclear whether their hepatic regulation of surplus copper resembles that of ruminants or monogastric species. They are therefore excluded from further discussion.

Wild herbivores in Africa have adapted to diverse, varying, and often harsh climatic conditions, with diet selection being opportunistic, inconsistent, and difficult to quantify. They usually have access to a wide variety of plant species to select from (Owen-Smith, 1999), making estimating their dry matter (DM) and copper intake practically impossible (Schiere & de Wit,1993). The nutritional management of wildlife, both in commercial farming and reservation areas, can be considered low-input, relying on what is locally produced and seasonally available (Schiere & de Wit, 1993). These systems are subject to periodic feed shortages (resource-induced seasonality), environmental stressors, and starvation, all of which will influence nutrient needs.

Pertinent information on relevant aspects of copper metabolism and availability is scattered across articles and books, and requires integration and harmonisation. Foundational insights into the digestive physiology of wildlife have been obtained from Van Soest's publications (e.g. Van Soest, 1994), and supplemented by the more recent publications of M. Clauss and collaborators (e.g. Clauss *et al.*, 2010). Where appropriate, sources that included data on related domestic animal species were used. Google Scholar was also used to search for and identify relevant publications.

Copper metabolism: bioavailability and homeostasis

Byrne & Murphy (2022) defined the bioavailability of trace elements as the proportion of an ingested element that is absorbed, transported, and converted to physiologically active forms at the site of action within the body. In quantitative terms, Windisch & Ettle (2008) defined bioavailability as the product of true absorption and metabolic utilisation, determined in the absence of homeostatic counter-regulation, i.e. in a deficiency supply status.

In ruminants, the efficiency of copper absorption – which is the key determinant of copper bioavailability – varies more than that of any other mineral, with copper bioavailability having an important influence on the occurrence of copper deficiency and toxicity in animals (Suttle, 2022). However, Suttle (2022) suggested that copper bioavailability in ruminant diets is not greatly impacted by the form of the copper, but more by antagonistic elements and fermentation processes in the rumen. Consequently, the copper concentration in a ruminant diet has limited diagnostic value (Suttle, 1994; Goff, 2018), unless a clearly deficient or toxic level in the diet is evident.

Copper bioavailability is affected by its solubility in the gastrointestinal tract, as only soluble minerals can interact with rumen microbes and other elements (EFSA Panel, 2016). Copper is typically found in the oxidised state (cupric, Cu^{2+}) in the diet, but is only transported in the reduced state (cuprous, Cu^{+}) across the small intestine's apical membrane. In the lower digestive tract, Cu^{2+} is reduced to Cu^{+} by reductase enzymes, aiding absorption (Goff, 2018; Nishito & Kambe, 2018). Waghorn *et al*. (1990) found that copper solubility increased as digesta moved from the rumen (pH 6.0–6.8) to the abomasum (pH 2.4–2.9). However, as digesta moved further through the small intestines, solubility decreased again, because of an increasing pH (Waghorn *et al*., 1990; Čadkovά *et al*., 2015). Suttle (1975a) demonstrated that copper availability was 21.4% when administered directly into the sheep abomasum, compared with only 3.7% when introduced into the rumen. Therefore, in ruminants, dietary factors that lower the ruminal pH increase copper bioavailability (Suttle, 2022). For instance, McCaughern *et al*. (2020) found that adding starch to the diets of lactating dairy cows lowered the ruminal pH, thereby increasing copper bioavailability and resulting in a higher hepatic copper concentration. To allow for factors affecting copper bioavailability in domestic ruminants, Suttle (2022) used copper bioavailability (A_{Cu}) values according to different nutritional scenarios to estimate copper requirements. Factors such as the assumed soluble carbohydrate content and the effect of the dietary fibre content on rumination and saliva flow were considered. Suttle (2022) suggested an A_{Cu} of 0.06 (6%) when dry, mixed rations were fed, an A_{Cu} of 0.03 (3%) for animals consuming green swards, and an A_{Cu} of 0.015 (1.5%) when diets contained >5 mg of molybdenum/kg of DM.

Various *in vitro* methods have been used to estimate the potential solubility of essential and toxic elements in ingested substances in the gastrointestinal tracts of humans and other monogastric species, measuring the so-called bioaccessibility of elements (Čadkovά *et al*., 2015; Roy *et al*., 2024). The quickest and cheapest method used is the simplified bioaccessibility extraction test (SBET), which simulates the highly acidic gastric phase of digestion in the stomach (Vasques *et al*., 2020). For example, Ettler *et al*. (2012) measured copper bioaccessibility in soils from mining areas in Zambia using the SBET, and reported that 80% to 83% of the total copper concentration was bioaccessible. Alternatively, the more practical two-stage physiologically based extraction test (PBET) simulates both the gastric and the more alkaline intestinal conditions in the gastrointestinal tract (Čadkovά *et al*., 2015). Čadkovά *et al*. (2015) recorded significant decreases in element bioaccessibility as digesta transitioned from the stomach to the intestines. In individual human diet ingredients, the bioaccessibility of copper, manganese, zinc, and lead in the gastric phase was between 25% and 53%, compared with 9% to 20% in the intestinal phase (Čadkovά *et al*., 2015). However, once elements with high theoretical bioaccessibility values have been identified in food substances, bioavailability still needs to be confirmed via more demanding *in vivo* trials (Čadkovά *et al*., 2015). It could be assumed that these bioaccessibility ranges would also be applicable to wild monogastric species. However, the gastric pH of herbivores is generally higher than the 1.5 to 2.0 pH used in most human bioaccessibility studies (Beasley *et al*., 2015; Roy *et al*., 2024), likely resulting in lower bioaccessibility in simulated herbivore conditions.

The liver is the main organ responsible for accumulating absorbed copper and for copper homeostasis in the body (Goff, 2018). However, there are significant differences in copper metabolism between ruminants and non-ruminants (Hill & Shannon, 2019). In monogastric species, homeostasis is activated once the dietary supply of the trace element changes from a deficient to a sufficient intake (Kirchgessner, 1993; Windisch & Ettle, 2008; Nishito & Kambe, 2018). Furthermore, in non-ruminants, the liver copper concentration is well regulated, largely by the biliary (endogenous) excretion of surplus copper, as copper binds to metallothionein in the liver and is excreted through the bile (Clarkson *et al*., 2020). In contrast, ruminants developed a systemic homeostatic mechanism of storing excess absorbed copper in the liver, with limited ability to regulate copper absorption and endogenously excrete copper through the bile into the digestive tract (EFSA Panel, 2016; López-Alonso & Miranda, 2020; Daniel & Martín-Tereso, 2025). However, Daniel & Martín-Tereso (2025) demonstrated in studies on cattle that apparent copper absorption is upregulated if the animal's trace element status is low. Consequently, within adequate dietary intake ranges, a linear increase in hepatic copper concentration with increased copper intake is observed in ruminants, providing a relatively reliable means of estimating the copper nutritional status in ruminants (Van Ryssen & Bath, 2024). However, domestic ruminant species differ significantly in their tolerance for excessive liver copper concentrations (Clarkson *et al*., 2020), and this is probably also the case among wild ruminants.

Studies on copper bioavailability have shown that in domestic ruminants with functional rumens, the true bioavailability of copper ranges from less than 1% to 10% of the dietary copper content (NRC, 2005). In sheep, it ranges from 1.4% to 12.8% (EFSA Panel, 2016; Suttle, 2022), while Goff (2018) quoted an apparent copper absorption of 4% for adult ruminants when consuming forages. In contrast, in non-ruminants, copper is comparatively well absorbed from the small intestine (Spears & Hansen, 2008). The NRC (2005) cited a textbook stating that in non-ruminants approximately 30% to 75% of dietary copper is absorbed, and López-Alonso & Miranda (2020) quoted a figure of up to 70%. Suttle (2022) used a copper bioavailability of 30% to estimate copper requirements for horses, and in pigs the apparent digestibility of innate copper in a basic diet was 38% to 44% (Jolliff & Mahan, 2013). Windisch & Ettle (2008) concluded that a true absorption range of trace elements in monogastric species of 30% to 40% reflects nutritional situations in practice.

Established factors affecting the bioavailability of dietary copper

Genetic differences in copper metabolism are well established among domestic species and breeds. For example, goats are more resistant to high dietary copper levels than cattle and sheep (Van Ryssen & Bath 2024). Distinct differences in copper metabolism are also evident among different breeds of sheep and cattle (López-Alonso & Miranda, 2020). The situation in African herbivores is not well established, although López-Alonso & Miranda (2020) noted that there seemed to be some species-related differences in copper requirements in deer. For monogastric species, it is noteworthy that the ARC (2005) stated that horses and rabbits (hindgut fermenters) seemed to be more resistant to copper toxicosis than pigs and poultry (simple stomached species).

In ruminants, elements that interact with copper and render it unavailable for absorption include molybdenum in conjunction with sulphur (which form indigestible thiomolybdates in the digestive tract and body), and sulphur on its own (which forms the insoluble copper sulphides CuS and Cu_2S in the digestive tract) (Suttle, 1994; EFSA Panel, 2016; López-Alonso & Miranda, 2020; Suttle, 2022). Another type of interaction involves competition for absorption, and interactions with iron (partly dependent on dietary sulphur), zinc, manganese, and cadmium can suppress copper absorption (Windisch & Ettle, 2008; Nishito & Kambe, 2018). Suttle (2004) suggested the following dietary ratios for ensuring marginal risks of copper deficiencies: sulphur:copper = 500–1000 mg/mg; iron:copper = 50–100 mg/mg; and molybdenum:copper = 0.3–1 mg/mg. Similarly, the EFSA Panel (2016) stated that a copper:molybdenum ratio of <1 indicates a high risk of copper deficiency, whereas a ratio of >3 is safe. Zinc is not a major factor affecting copper absorption, unless the diet contains at least 20-fold more zinc than recommended (EFSA Panel, 2016; NRC, 2001), or >200 mg zinc/kg DM (Suttle, 2022). Goff (2018) also stated that the effect of iron on copper metabolism is negligible until the dietary iron content exceeds 500 mg/kg. However, Suttle (2022) cited research showing a reduction in A_{Cu} at a dietary iron content of 250 mg/kg DM. Inorganic and organic sulphur are equally effective at interacting with copper (Suttle, 1975b). These limits for dietary zinc and iron should be considering when evaluating factors affecting copper absorption.

Goff (2018) noted that the rumen presents a significant barrier to mineral absorption, a challenge that monogastric animals do not face. Pearse *et al.* (1999) demonstrated that copper metabolism in horses, and likely other hindgut fermenters, is not affected by high molybdenum intakes because the interaction between copper and molybdenum occurs in the hindgut, after most molybdenum has already been absorbed (Suttle, 2022). According to Suttle (2022), the interaction between copper and sulphur also largely depends on the release of sulphur from sulphur-containing amino acids during rumen fermentation, which is not relevant in monogastric species. The EFSA Panel (2016) highlighted that in the gastrointestinal tracts of monogastric animals, phytates from cereals and seeds bind to positively charged ions such as Cu^{2+} and Zn^{2+}, rendering them less available for absorption and interactions. However, free-ranging wildlife species have minimal access to cereals and are thus less exposed to phytates. In monogastric species, copper can interact with ascorbic acid and elements like iron, zinc, and calcium (NRC, 2005; Kienzle & Zorn, 2006; Windisch & Ettle, 2008), as well as with non-essential elements such as cadmium, silver, and lead (Baker & Ammerman, 1995). Additionally, Baker & Ammerman (1995) noted that substances of high chelating and reducing potential could decrease copper bioavailability in monogastric species, while Čadkovά *et al.* (2015) speculated that variability in bioaccessibility may be related to copper complexing with a wide spectrum of organic ligands with various levels of degradability by digestive enzymes. According to Goff (2018), elements can form complexes with fibre or other dietary components, limiting solubility. In the abomasum, acidic conditions may solubilise some complexes, but incomplete dissociation may occur if the digesta does not spend sufficient time in this part of the digestive tract (Goff, 2018).

While hepatic copper concentrations in ruminants increase linearly with increasing dietary copper concentrations, in pigs and poultry they remain constant and only rise significantly when dietary copper exceeds 150 mg/kg in pigs and 250 mg/kg in poultry. These values represent the maximum tolerance levels (MTL) for these species (NRC, 2005; EFSA Panel, 2016), or 50 times their requirements (López-Alonso & Miranda, 2020). Similar MTLs have been recorded for other poultry species (NRC, 2005; EFSA Panel, 2016). This phenomenon could be explained by an overloading of the homeostatic system of biliary excretion of surplus copper in the liver, or could be related to the process of paracellular absorption (Goff, 2018). Goff (2018) described paracellular absorption as the process that occurs when the concentration of an element in solution in the small intestine is significantly greater than the concentration of that element in the extracellular fluid. This concentration gradient causes the element to be pushed via solvent drag across the tight junctions of the intestinal wall and into the bloodstream. The paracellular absorption of elements is most likely to occur when animals consume diets containing high concentrations of an element, as it is dependent on large concentration gradients. In a survey of liver mineral concentrations in captive rhinoceroses, Dierenfeld *et al.* (2005) reported unusually high hepatic copper levels in Indian *(Rhinoceros unicornis)* and white rhinoceroses (170 ± 296 and 83 ± 88 mg copper/kg wet weight, respectively), compared to only 5–6 mg/kg wet weight in other rhinoceros species. This may reflect the effects of enhanced paracellular absorption, although unusual trace element metabolism has been previously documented in rhinoceroses, such as the iron overload disorder observed in captive black rhinoceroses by Mohieddin (2021).

Probable factors affecting copper bioavailability

Since browse differs from grass in fermentation characteristics and often contains secondary plant metabolites that necessitate defensive adaptations in animals, such as specialised salivary properties, the availability of copper in browse may differ from that in grass (Clauss *et al*., 2010). For mature wild ruminant species weighing from 2 kg to over 1000 kg, variations in copper metabolism can be expected. Striking differences have been recorded in the mean retention time of food in the digestive tract between feeding types, with evidence that in very small ruminants some of the digesta might escape ruminal fermentation (Hoppe, 1984). Such differences would have significant effects on the solubility of copper in the small intestines.

Ruminants have been classified into two morphophysiological digestive types: the cattle-type (grazers and intermediate feeders) and the moose-type (strict browsers) (Clauss *et al*., 2010). The rumen content of the cattle-type exhibits distinct stratification, including a coarse fibre mat and a gas layer, whereas the moose-type shows little to no stratification. The key physiological difference between these two types is the ratio of small particles to fluid retention in the reticulo-rumen. In moose-types, both digesta phases (particles and fluid) move similarly through the reticulo-rumen, whereas in cattle-types, the fluid moves much faster than the particle phase (Przybylo *et al*., 2019). To evaluate digesta kinetics, the passage rates of fluid and particles are measured using internal and external markers (Przybylo *et al*., 2019). Moose-type ruminants also exhibit a lower frequency of rumination compared with cattle-types (Lauper *et al*., 2013), resulting in reduced saliva flow in moose-type species (Clauss *et al*., 2021). Clauss *et al*. (2011) suggested that the fast fermentation pattern in browsers probably contributes to the lower pH in the rumen fluid of browsers compared with grazers. Moose-types have a lower rumen throughput than cattle-types, with higher fluid throughput linked to a greater buffering capacity and a higher rumen pH (Clauss *et al*., 2010; 2011). A survey of rumen pH values across various game species by Ritz *et al*. (2013) concluded that browsing species typically have a lower rumen pH, whereas grazing species exhibit a higher pH because of their higher fluid and saliva throughput. For example, the average rumen pH for African browsers was around 5.78, while grazers had a pH of 6.68 (Ritz *et al*., 2013). Since rumen pH affects copper availability, this difference in pH could influence copper solubility in the forestomach of these digestive types. However, variation exists even within strict browsers. For instance, the greater kudu (*Tragelaphus strepsiceros*), although classified as a strict browser, exhibits physiological traits that distinguish it from other species within the moose-type group (Przybylo *et al*., 2019; 2022).

Sahu & Kamra (2002) reviewed the microbial ecosystem of the gastrointestinal tracts of wild herbivorous animals world-wide. The diverse feeding habits of wildlife and the chemical composition of the diet causes large variations in the composition of microbial populations in the rumen. In a series of experiments, Ivan (1988) demonstrated that the defaunation of the rumen in sheep led to an increase in the absorption of copper and elevated copper concentrations in the liver, compared with faunated sheep. According to Goff (2018), the proteins of ciliated protozoa in the rumen have an affinity for some elements, such as copper. Copper bound to these proteins is insoluble in rumen fluid and may not be liberated during the passage through the distal portion of the digestive tract. Furthermore, Suttle (2022) explained that rumen protozoa generate S^{2-}, which potentiates antagonism with molybdenum and iron, or precipitates copper as CuS, which remains unabsorbed. Sahu & Kamra (2002) cited research that found that some individuals in a deer species were protozoa-free. According to Hoppe (1984), the rumens of the dik-dik (*Madoqua guentheri*), suni (*Nesotragus moschatus*), and duiker species contain no or very low concentrations of protozoa, although Clauss *et al*. (2011) noted that other studies had reported the presence of protozoa in some of these species. In a comprehensive literature review on protozoal fauna in wild ruminants, Clauss *et al*. (2011) concluded that differences in ruminal pH and related effects in the rumen may have a considerable influence on the species of protozoa present in ruminant species. The presence or absence of protozoa in the rumen could contribute to differences in the bioavailability of dietary copper in different ruminant species.

Extensive research into the contribution of external abrasives, such as dust, grit, sand, and fine silt, to dental wear in herbivores has also been conducted (Kaiser *et al*., 2013; Merceron *et al*., 2016; Sanson *et al*., 2017; Hatt *et al*., 2019). However, Hatt *et al*. (2019; 2020) demonstrated that soil, assumed to be an external abrasive, is not regurgitated and masticated during rumination (i.e. heavy-duty chewing versus ingestive mastication). Instead, it is washed off the ingesta in the reticulo-rumen and passes through the fore-stomachs to accumulate in the acidic abomasum (glandular stomach), which is the primary site of sand impaction in ruminants. It could be assumed that the acidic conditions in the abomasum would solubilise these minerals and increase the bioaccessibility of copper, iron, and other elements in the soil, as described by Čadková *et al*. (2015), depending on the duration of the soil's stay in the abomasum. This suggests that ingested soil could be a good source of available trace elements to ruminants (Abrahams, 2012), more than usually assumed. Hansen & Spears (2009) measured the bioaccessibility of elements in soil exposed to acidic conditions during silage fermentation and recorded significant increases in the water-soluble iron concentration, depending on soil type and the level of soil inclusion. However, they pointed out that the increased bioaccessibility of iron in soil pre-exposed to acidic conditions may counter the intestinal absorption of trace elements such as copper and manganese (Hansen & Spears, 2009). An interesting possibility is that when very alkaline soils – such as those found in South Africa's Northern Cape province – are ingested, they could accumulate in the abomasum and potentially buffer or neutralise the abomasal pH and thereby reduce the solubility of copper.

Considerations in estimating copper allowances

Free-ranging game animals primarily rely on natural vegetation as their main source of essential nutrients such as copper, with soil ingestion also contributing to their mineral intake (Abraham, 2012). Van der Ent *et al*. (2013) reported that the copper concentration in plant leaves is typically maintained within a narrow range of around 10 mg copper/kg DM, even on metalliferous soils, and that the optimal range for plant copper concentrations is considered to be 5–30 mg copper/kg DM (Shabbir *et al*., 2020; Kumar *et al*., 2021). Because of the wide diversity of wildlife species in Africa and the broad range of plant species they consume, accurately determining the actual copper intake and precise copper requirements of individual animals or species is not feasible. In practice, the values often referred to as requirements could be more accurately described as recommendations (White, 1996). Recommendations reflect the estimated amounts of a nutrient needed by animals living under variable environmental conditions, taking into account fluctuations in feed intake, production levels, and nutrient bioavailability, with the possible inclusion of a safety margin (White, 1996; Weiss, 1998). In the absence of definitive data for wildlife, the copper requirements of domestic animals of similar body size and digestive physiology can serve as useful references. However, even the published copper requirements of domestic ruminants provide only rough estimates of dietary needs (Suttle, 2022), since there is considerable variation in copper recommendations for domestic ruminants among experts and across countries (Suttle, 1994; White, 1996; Suttle, 2022).

Animals require specific amounts of nutrients daily, typically measured in grams or kilograms. The dietary concentration of these nutrients is usually calculated based on the amount of feed consumed per day, either on a DM or an as-fed basis (Windisch & Ettle, 2008). It has been calculated that in herbivores, the daily food intake as a fraction of body weight decreases linearly as body weight increases (Owen-Smith, 1999), assuming no restrictions in resource availability. For example, medium sized antelopes will typically eat 1.5%–2.5% of their body weight per day, whereas small antelopes eat 3%–4% of their body weight, and large herbivores such as elephants and rhinoceroses eat 0.8%–1.5% (Owen-Smith, 1999; Smit, 2018). This implies that if copper requirements for maintenance are expressed in terms of the daily DM intake of a species, copper concentrations in the diet would decrease with an increase in the mean body weight of the species. However, in comparison with ruminants, equids (e.g. horses) have a higher feed intake, partly due to differences in digestive strategies (Clauss, 2013). Ruminants have a low-intake, slow-throughput strategy, while hindgut fermenters employ a high-intake, fast-throughput digestion strategy, resulting in shorter digesta retention times (Duncan *et al*., 1990; Clauss, 2013). Smit (2018) reported that the zebra *(Equus quagga burchellii)* consumes 4.1% of its body weight. Similarly, Hummel *et al*. (2020) calculated that a 600 kg horse has a DM intake 68% higher than that of a comparable-sized cow. Therefore, if the amount of copper required for the maintenance of a zebra weighing 216 kg is the same as that of a sable antelope *(Hippotragus niger)* weighing 215 kg and taking in 2.8% of its body weight (Smit, 2018), the required copper concentration in the zebra's diet would be substantially lower than that of the antelope.

Nutrient requirements also depend on factors such as production levels and growth stages (White, 1996). In wildlife, the production level rarely exceeds the animal's maintenance needs, even for milk production. Therefore, the copper requirements of wildlife are likely to be close to their maintenance needs, with an additional activity (work) factor (White, 1996; Suttle, 2022). However, Girard (2008) and Goff (2018) have suggested that current recommendations for copper intake may be inadequate for optimal immunity. Furthermore, Moyo *et al*. (2017) noted that wildlife on tropical African grasslands often face feed shortages because of droughts. Starvation results in the retention of digesta for longer durations, with slower rates of passage than during periods of abundance (Moyo *et al*., 2017). However, elevated soil intake could probably compensate to some extent for the reduced intake of minerals from vegetation during periods of food scarcity (Abrahams, 2012).

Gould & Kendall (2011) noted that experiments in ruminants have shown that, in the absence of antagonists, the absolute dietary requirement for copper was 1.6 mg/kg, and López-Alonso & Miranda (2020) stated that domestic ruminants maintain adequate copper status with dietary levels as low as 5 mg/kg. The EFSA Panel (2016) published copper requirements ranging from 5 to 25 mg copper/kg DM for non-productive caprine and ovine species. It should be noted that Daniel & Martín-Tereso (2025) criticised that the current metal feeding recommendations for cattle assumes fixed absorption efficiencies when calculating gross requirements. Suttle (2022) addressed this for copper, and based estimates of the dietary copper requirements of sheep and cattle on copper absorbability values determined under different nutritional scenarios, for instance, using an A_{Cu} of 0.06 for normal green swards and of 0.015 for swards rich in molybdenum.

For hindgut fermenters, copper requirements for horses, known as 'horse normal ranges', can provide guidance (Dierenfeld *et al*., 2005). However, Kienzle & Zorn (2006) cautioned that the copper requirement values for horses are not unequivocally agreed upon, as many factors can influence requirements (Hintz, 1996). Published requirements for horses range from 6 to 12.5 mg copper/kg (EFSA Panel, 2016), with 10–12 mg/kg DM being recommended for growing horses (Hintz, 1996). For captive herbivores (zoo animals), including hindgut fermenters, Lintzenich & Ward (1997) proposed dietary copper requirements of between 6 and 9 mg/kg (on a 90% DM basis). For captive herbivores such as rhinoceroses in zoos, the European Association of Zoos and Aquariums recommended a copper level of 10 mg/kg DM (Ricketts *et al*., 2020).

Conclusions

It is virtually impossible to conduct controlled studies on free-ranging wildlife, and most available research is thus based on observations or opportunistic investigations made during abnormal events such as poisoning or deficiency outbreaks. Valuable studies are conducted on wild animals in confinement, during which basic principles can be established, but these remain limited by the difficulty of replicating natural conditions, especially in the case of browsers (Dierefeld, 1997). Consequently, proposing future research directions is challenging, although researchers can be encouraged to take advantage of opportunities as they arise.

It is noteworthy that the predicted copper requirements for ruminants and equids consuming roughage diets are quite similar, around 10 mg/kg. However, from this review it can be concluded that the copper requirements of equids and possibly other hindgut fermenters should be substantially lower than that of ruminants:

- It is generally accepted that in ruminants with active rumens, between 1% and 10% of dietary copper is available for absorption, while in monogastric species the bioavailability of copper exceeds 30%. This should amount to a significantly lower dietary requirement for copper in non-ruminants compared with ruminants.
- In free-ranging hindgut fermenters, antagonists to copper absorption are usually fewer and less prominent than in ruminants, and phytates are usually not present in the diets of free-ranging herbivores.
- At a comparable body weight, the voluntary feed intake per day of equids is substantially higher than that of ruminants. Consequently, the quantity (milligrams) of copper required per unit of body weight might be similar for equids and ruminants of the same body weight, but when expressed as a proportion of the daily DM intake, the copper concentration/kg DM in the equid diet should be lower than that in the ruminant diet.
- Conversely, the higher rate of passage of digesta through the digestive tract of hindgut fermenters, compared with ruminants, could result in decreased copper absorption in non-ruminants. However, while this is applicable to macro-nutrients, it is not necessarily applicable in the case of micro-nutrients.

These points suggest that non-ruminants are generally able to tolerate lower levels of dietary copper than ruminants before showing signs of copper deficiency. Compared with ruminants, non-ruminants can also tolerate much higher levels of copper intake, as demonstrated by studies in horses (Belli *et al*., 2021) and by common feeding practices in pigs and poultry (Hill & Shannon, 2019). It is concluded that incidences of both copper deficiency and copper toxicity in monogastric species, including hindgut fermenters, are unlikely under free-ranging foraging conditions in southern Africa. However, limited, if any, information seems to be available on copper metabolism in the large hindgut fermenters, such as the elephant and rhinoceros species.

Van der Ent *et al*. (2013) stated that forages contain, on average, 10 mg copper/kg DM, and this seems to be a standard assumption. If this is correct, the innate copper present in plants would, in general, satisfy the copper requirements for maintenance of free-ranging wildlife. However, advisers should consider the various possible sources of both copper and copper antagonists in each situation, such as water, plant bark and roots, flowers, seeds and pods, and soil. For example, Sanson & Read (2017) pointed out that buffalo herds raise clouds of dust that can be ingested when grazing. In comparison, minimal dust is released when single or small groups of animals are foraging. Dietary antagonists to copper are major factors affecting copper bioavailability, especially molybdenum, but also iron and sulphur. Unfortunately, chemical analyses would be required to confirm the presence of antagonists.

A general guideline to advisers would be that smaller-bodied ruminant species can meet their copper maintenance requirements on diets containing lower copper concentrations per kilogram of DM than larger species, because they consume more DM relative to their body weight than larger species. However, copper metabolism in very small ruminants, particularly frugivores, remains poorly understood, as no domestic analogues are available for comparison. A similar gap in knowledge exists for giraffe species, whose genetic background differs substantially from those of bovid species.

In ruminants, the bioavailability of copper is strongly influenced by the pH of the rumen contents, with dietary factors that lower rumen pH generally enhancing copper absorption. Differences in the bioavailability of copper between diet types, as reported by Suttle (2022), should thus also exist between grazers and browsers, owing to their distinct dietary preferences. They should also exist between cattle-type and moose-type ruminants, because of the morphophysiological differences in the digestive processes of these two types.

A notable advantage in ruminants is that, within the range of adequate copper intakes, liver copper concentrations tend to increase linearly with the level of copper intake. As a result, liver copper concentrations may serve as relatively reliable indicators of the copper nutritional status in ruminants, as suggested for African wild ruminants (Van Ryssen & Bath, 2024). However, it remains to be confirmed whether this relationship holds true across all ruminant species, particularly those at the extremes of the ruminant spectrum. Species-specific guidelines for wild ruminants have yet to be developed.

Authors' contributions

J.B.J.v.R. did the literature search and wrote the initial copy. G.F.B. revised, edited, and proofread the manuscript.

Conflict of interest declaration

The authors declare no conflicts of interest.

Ethical approval

The authors declare that this submission is in accordance with the principles laid down by the Responsible Research Publication Position Statements, as developed at the 2nd World Conference on Research Integrity in Singapore, 2010.

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