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SHORT COMMUNICATION

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Coprophagy of African wild dog faeces by spotted hyaenas and hooded vultures in Mana Pools National Park, Zimbabwe

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1 | INTRODUCTION

Coprophagy is defined as the consumption of one's own faeces (autocoprophagy) or the faeces of other individuals of the same or other species (allocoprophagy) (Soave & Brand, 1991). Coprophagy has been described for a wide range of species and usually serves as an additional source of nutrients or as a means to acquire intestinal bacterial microflora (Graczyk & Cranfield, 2003; Soave & Brand, 1991). In captive and domesticated animals, coprophagy has also been associated with mental stress, anxiety and boredom (Boze, 2010). The consumption of one's own faeces or faeces of conspecifics (intraspecific coprophagy) is common, in particular for rodents and lagomorphs (Soave & Brand, 1991). However, among vertebrates, the consumption of faeces of another species (interspecific coprophagy) is relatively rare (Fish et al., 2007; Reading et al., 2017).

The African wild dog (*Lycaon pictus*) is an endangered social carnivore which hunts in packs for medium to large prey (Woodroffe & Sillero-Zubiri, 2020). In most of their current range, African wild dogs coexist with larger competing carnivores, such as spotted hyaenas (*Crocuta crocuta*). Spotted hyaenas have been found to follow African wild dogs during the hunt to steal (kleptoparasitism) or scavenge from its kills (van der Meer et al., 2011). Another species which accompanies African wild dogs to scavenge is the critically endangered (BirdLife International, 2017) hooded vulture (*Necrosyrtes monachus*) (Reading et al., 2017). While observing a pack of African wild dogs on a kill, Reading et al. (2017) witnessed hooded vultures consuming African wild dog faeces, which is the first published record of this behaviour. In this study, we describe the frequency of coprophagy of African wild dog faeces by hooded vultures and spotted hyaenas in Mana Pools National Park, Zimbabwe, and the circumstances under which this behaviour occurred.

2 | METHOD

2.1 | Study area

Mana Pools National Park (MPNP) is a 2 196 km^2 protected area in northern Zimbabwe (15°56′S, 29°27 E). MPNP is managed by the Zimbabwe Parks and Wildlife Management Authority and utilised for photographic safaris. Mean annual rainfall is ca. 706 mm, with a wet season from November to March. July is the coldest month (mean minimum temperature 10.7°C) and October the hottest (mean maximum temperature 39.7°C). Main vegetation types in MPNP are *Colophospermum mopane* woodland, *Faidherbia albida* woodland, *Brachystegia–Julbernardia* woodland and *Commiphora–Combretum* thicket. MPNP is situated along the Zambezi river, which is the main permanent water source (ZPWMA, 2009). Apart from African wild dog, the park is home to brown hyaena (*Parahyaena brunnea*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), lion (*Panthera leo*), spotted hyaena (*Crocuta crocuta*) and a variety of herbivorous species, such as buffalo (*Syncerus caffer*), eland (*Tragelaphus oryx*), impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus ellipsiprymnus*) and zebra (*Equus quagga*) (ZPWMA, 2009). In 2019, MPNP experienced a severe drought receiving an annual rainfall of ca. 302 mm only (Mutsaka, 2019).

2.2 | Data collection and analyses

As part of a long-term ecological study (van der Meer et al., 2019), data from six radio-collared African wild dog packs were collected between September 2017 and November 2020, including both the

denning season (May–August), when pups are too small to follow the pack and movement is restricted because the pack needs to return to the den (Malcolm & Marten, 1982), and the nomadic season. A receiver and directional antenna were used to locate and keep track of a pack. Continuous observations were made from a vehicle for as long as practically feasible. The openness of the study area and the extensive road network, which African wild dogs use to travel and rest, usually allowed us to keep pace with the pack and follow their (hunting) movements visually and/or by radiotelemetry. A total of 185 (hunt) observations, collected over 150 days at dusk and/or dawn, were used to describe interactions between African wild dogs and spotted hyaenas or hooded vultures. When an interaction was observed, records were taken of the date, time, type of interaction (coprophagy, scavenging or kleptoparasitism), number of individuals present and/or interacting and whether or not the African wild dogs actively tried to chase the spotted hyaenas or hooded vultures away. For spotted hyaenas, body condition was scored on a scale of one (very poor) to five (very good). We used a two-tailed Fisher's exact test to determine whether occurrence of coprophagy (versus scavenging and not present) by spotted hyaenas or hooded vultures was affected by seasonality (denning versus nomadic season, dry versus wet season), the severe 2019 drought (drought versus no drought) and time of day (am versus pm). A Mann–Whitney *U* test was used to analyse whether there was a difference in pack size (adults + yearlings) and the number of spotted hyaenas/hooded vultures present/interacting between coprophagy and scavenging, and whether this affected tolerance by African wild dogs. We also used a Mann–Whitney *U* test to determine if there was a difference in body condition between spotted hyaenas which engaged in coprophagy and those scavenging. Statistical analyses were performed with SPSS software version 20.0 (SPSS Inc., Chicago, IL, USA). The Research Council of Zimbabwe and the Zimbabwe Parks and Wildlife Management Authority provided clearance for this study under permit no SC/9 02935, 03446, 03778 and 23(1) (C) (II) 3/2017, 17/2018, 4/2019, 07/2020.

3 | RESULTS

When spotted hyaenas were present ($n = 90$), they engaged in coprophagy of African wild dog faeces in 41.1% of the cases (Figure 1a) and scavenging took place 26.6% of the observations, while we observed three cases of kleptoparasitism. When hooded vultures were present ($n = 58$), they engaged in coprophagy in 65.5% of the cases (Figure 1b) and scavenging took place 19.0% of the observations. For spotted hyaenas, coprophagy was not related to the denning or nomadic season ($p = 0.48$), wet or dry season ($p = 0.92$), time of day ($p = 0.87$) or severe drought ($p = 0.22$). African wild dog pack size (adults + yearlings) during coprophagy by spotted hyaenas did not differ from pack size when spotted hyaenas were scavenging ($p = 0.86$, $U = 487.00$, $z = -0.17$) or absent ($p = 0.19$, $U = 1196.00$, $z = -1.31$). For hooded vultures, coprophagy was not related to the denning or nomadic season ($p = 0.34$), wet or dry season ($p = 0.89$), time of day ($p = 0.07$) or severe drought ($p = 0.12$). African wild dog pack size (adults + yearlings) during coprophagy by hooded vultures did not differ from pack size when hooded vultures were scavenging ($p = 0.24$, $U = 161.00$, $z = -1.17$) or absent ($p = 0.56$, $U = 96.00$, $z = -0.63$). Overall, mean African wild dog pack size (adults + yearlings) was 7.53 ± 3.20 (mean ± SD) individuals.

Coprophagy by spotted hyaenas took place while African wild dogs were resting (35.1%) but also when they were on a kill (18.9%), hunting (21.6%) or engaged in other activities (24.3%), whereas coprophagy by hooded vultures predominantly occurred when African wild dogs were resting (78.9%). Most coprophagy by spotted hyaenas (93.5%) and hooded vultures (83.3%) happened when they were already following (present before a kill was made) an African wild dog pack. However, we observed only six cases in which spotted hyaenas combined coprophagy with scavenging, whereas such combined behaviour was not observed for hooded vultures. There were six cases in which both spotted hyaenas and hooded vultures consumed faeces in the same observation of the same African wild dog pack.

The number of spotted hyaenas present during coprophagy was 3.57 ± 3.65 (mean ± SD), with a minimum of one and a maximum of eighteen individuals, which was not significantly different from the number present while scavenging ($p = 0.72$, $U = 455.50$, $z = -0.37$). However, within a group of spotted hyaenas, only one to two individuals engaged in coprophagy. The number of spotted hyaenas which took part in coprophagy was 1.26 ± 0.44 (mean ± SD), which was lower than the number of spotted hyaenas interacting when scavenging ($p < 0.01$, $U = 211.50$, $z = -3.97$). Body condition of spotted hyaenas which engaged in coprophagy did not differ from those that scavenged ($p = 0.26$, $U = 94.00$, $z = -1.28$) and was poor (43.8%) or medium (46.9%) but seldom

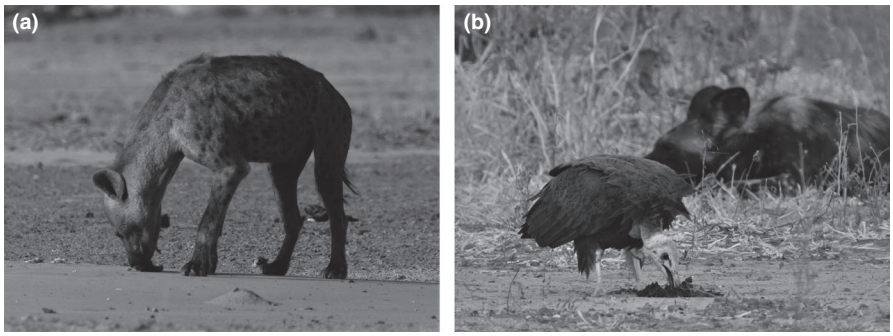

FIGURE 1 Coprophagy of African wild dog faeces by spotted hyaena (a) and hooded vulture (b) (photo credit: Thomas Mutonhori)

good (9.4%). The number of hooded vultures present during coprophagy was 4.63 ± 3.15 (mean ± SD), with a minimum of one and a maximum of seventeen individuals, which was not significantly different from the number present during scavenging ($p = 0.18$, $U = 121.00$, $z = -1.37$). The number of hooded vultures which took part in coprophagy was 3.84 ± 2.94 (mean ± SD), with a minimum of one and a maximum of seventeen individuals, which was similar to the number of individuals interacting when scavenging ($p = 0.10$, $U = 95.50$, $z = -1.67$). African wild dogs only chased hooded vultures during 16.3% of all interactions. However, they were less tolerant towards spotted hyaenas. Regardless of pack size ($p = 0.88$, $U = 168.00$, $z = -0.18$), African wild dogs chased spotted hyaenas during 70.7% of all interactions, and 65.4% of the coprophagy interactions. In general, African wild dogs were less tolerant towards large groups (4.69 ± 3.87 (mean ± SD)) than small groups (2.50 ± 2.51 (mean ± SD)) of spotted hyaenas ($p = 0.02$, $U = 94.50$, $z = -2.31$). When spotted hyaenas engaged in coprophagy, African wild dogs also more often chased after large groups (4.41 ± 3.37 (mean ± SD)) than small groups (2.00 ± 1.66 (mean ± SD)) of spotted hyaenas ($p = 0.04$, $U = 39.00$, $z = -2.07$).

4 | DISCUSSION

Coprophagy of African wild dog faeces by spotted hyaenas and hooded vultures in particular was relatively common and mostly occurred when spotted hyaenas or hooded vultures were already following an African wild dog pack. Although this suggests this behaviour is opportunistic, coprophagy was rarely observed in combination with other behaviours. Furthermore, hooded vultures especially often engaged in coprophagy when they accompanied resting African wild dog packs, suggesting they may be attracted to resting packs primarily to consume faeces. Coprophagy does not present a competitive threat to African wild dogs, and packs generally tolerated this behaviour by hooded vultures and spotted hyaenas, especially when spotted hyaena group size was small.

When wild vertebrates consume or feed on faeces of other species, the reason for this behaviour is usually related to the acquisition of energy and/or nutrients (Fish et al., 2007; Gallant, 2004; Negro et al., 2002). African wild dogs hunt their own prey and rarely scavenge (Pribyl & Crissey, 1999). The daily faecal output of raw meat diets contains ca. 82 kcal and 18% crude protein (Iennarella-Servantez, 2017). Based on an energy density of 5.0 kcal/g (Bosch et al., 2015) and a consumption of 4 kg carcass/day for spotted hyaena (Kerr et al., 2007) and 0.35 kg/day for hooded vulture (Brink et al., 2020), coprophagy of a raw meat diet scat provides ca. 1% and 12% of the daily energy intake of spotted hyaena and hooded vulture, respectively. Although African wild dog scats could provide a source of energy for hooded vultures, for spotted hyaenas, the energetic gain of coprophagy seems insignificant. Coprophagy by spotted hyaena in particular is therefore more likely to be related to the acquisition of nutrients. This is supported by the fact that coprophagy by hooded vultures and spotted hyaenas did not occur less in 2019, when a severe drought resulted in an abundance of carcasses and therefore increased feeding opportunities for scavengers (Mutsaka, 2019).

Faeces can provide a range of nutrients, for example, vitamins (e.g., vitamin B), minerals (e.g., iron and sulphur), proteins, amino acids and trace elements (e.g., nitrogen) (Soave & Brand, 1991). Coprophagy is an essential source of nutrients for growth, development and maturation in coprophagous species (Soave & Brand, 1991), whereas coprophagy in noncoprophagous species is generally related to diets deficient in proteins, amino acids and vitamins (Flurer & Zucker, 1988; Graczyk & Cranfield, 2003; Soave & Brand, 1991). The fact that specific individuals within a group of spotted hyaenas engaged in coprophagy, and body condition of those individuals was generally poor to medium suggests these individuals might try to meet a nutritional deficiency. Further research is required to determine the content of African wild dog faeces and the potential nutritional benefits for spotted hyaenas and hooded vultures.

Although coprophagy is a new aspect, the relationship between spotted hyaenas and African wild dogs is well-studied and acknowledged in the African wild dog's conservation strategy (van der Meer et al., 2011; Woodroffe & Sillero-Zubiri, 2020). Less is known about the relationship between hooded vultures and African wild dogs. However, based on Reading et al. (2017) and our findings, hooded vultures seem to form close associations with African wild dogs. Although further studies will have to shed light on the exact nature of this association, it may play a role in the survival of hooded vultures and should therefore be considered in the species' conservation strategy.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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