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Short communication

Iberian wild goat coprophagy on dove guano. A case report and insights from food analysis

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ABSTRACT

Heterospecific coprophagy. i.e., the consumption of excreta of other species, is reported and documented for the first time for Iberian wild goat *Capra pyrenaica* Schinz, 1838 and is discussed in light of the nutritional composition of the excreta. Two adult female goats were observed consuming guano of rock dove *Columba livia* Gmelin, 1789 in March 2021 in the Natural Park of Guara. The chemical composition and feed value of the dove guano consumed by goats was analyzed using standard methods of food analysis. The guano had moderate energy content and high concentrations of nitrogen-compounds that are convertible into protein. It was also rich in macronutrients such as calcium, phosphorus, sodium and sulfur, some of which (namely phosphorus) may be deficient for goats in calcareous environments such as the study area. High levels of sodium and possibly of guanine can cause hedonistic responses to salty and umami flavors that may contribute and reinforce this feeding habit. The guano was affected by desiccation and aging resulting from outdoor exposure, which might have also decreased its degree of pathogenicity. We hypothesize that female Iberian wild goats could be stimulated by guano in the second half of their pregnancy period, when their protein requirements increase. Heterospecific coprophagy has been documented in a wide range of mammals indicating it may be an important feeding activity, but it is still poorly described and understood. Its causes, consequences and relevance should deserve more attention to better understand their feeding ecology. This has to be faced under a multidisciplinary approach.

1. Introduction

Coprophagy is the ingestion of fecal material, either of the animal's own (auto-coprophagy) or of individuals of the same species (allo-coprophagy) or other species (heterospecific coprophagy). Auto-coprophagy is well-known in non-ruminant herbivorous mammals such as lagomorphs, rodents and primates which re-ingest their feces to further digest the plant matter and maximize the nutrient extraction (Hörnicke and Björnhag, 1980; Soave and Brand, 1991; Hirakawa, 2001). Allo-coprohagy has been mostly reported in young individuals of herbivore species of, for example, rodents (Dyer, 1998), primates (Mouele et al., 2022) and marsupials (Osawa et al., 1993), to which the adults' excreta can serve as a transitional food during weaning from milk to vegetable diet and provide with the gut microbiota required to properly digest complex carbohydrates. In comparison, reports on heterospecific coprophagy in wild mammals are scarce, although this behavior is possibly underreported because of the challenge in documenting it (Speakman et al., 2021; Waggershauser et al., 2022).

Table 1 provides a compilation of studies reporting heterospecific coprophagy in wild mammals including ruminant and non-ruminant artiodactyls, primates, rodents, sloths, marsupials and carnivores. Most of these studies relate coprophagy to the acquisition of energy and nutrients. By eating the feces of other animals, herbivores obtain access to food resources such as fruits not easily available to the species (Ranade and Prakash, 2015) and seeds softened and/or detoxified by their passage through the gut (Magliocca et al., 2003; Krief et al., 2005; Fish et al., 2007; Johnson et al., 2012). Feces of other species may serve as an alternate source of highly-digestible food in periods of increased nutrient needs such as lactation (Nishikawa and Mochida, 2010). Carnivore feces usually contain undigested remains that other species can take advantage of during periods of food scarcity (Livingston et al., 2005; Leuchtenberger et al., 2012; Laurentino et al., 2019).

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Table 1
A compilation of studies documenting heterospecific coprophagy in wild mammals.

Reference	Species eating feces	Species providing feces
Van der Wal and Loonen (1998)	Reindeer *Rangifer tarandus*, (Linnaeus,1758)	Barnacle goose *Branta leucopsis* (Bechstein, 1803)
Magliocca et al. (2003)	Red riverhog *Potamochoerus porcus* (Linnaeus, 1758) and sitatunga *Tragelaphus spekii* Speke, 1863	African forest elephant *Loxodonta cyclotis* (Matschie, 1900)
Krief et al. (2005)	Eastern chimpanzee *Pan troglodytes schweinfurthii* (Giglioli, 1872)	African bush elephant *Loxodonta africana* (Blumenbach, 1797)
Fish et al. (2007)	Ring-tailed lemur *Lemur catta* Linnaeus, 1758	Humans *Homo sapiens* Linnaeus, 1758, cattle *Bos taurus* Linnaeus, 1758 and feral dogs *Canis lupus* subsp. *familiaris* Linnaeus, 1758
Masseti (2009)	Wild goat *Capra aegagrus* Erxleben, 1777	Yellow-legged gull *Larus michahellis* J. F. Naumann, 1840
Nishikawa and Mochida (2010)	Sika deer *Cervus nippon* Temminck, 1838	Japanese macaque *Macaca fuscata yakui* Kuroda, 1941
Heymann et al. (2011)	Hoffmann's two-toed sloth *Choloepus hoffmanni* Peters, 1858	Humans *Homo sapiens* Linnaeus, 1758
Johnson et al. (2012)	Olive baboon *Papio anubis* (Cuvier, 1824)	African bush elephant *Loxodonta africana* (Blumenbach, 1797)
Leuchtenberger et al. (2012)	Crab-eating fox *Cerdocyon thous* (Linnaeus, 1766) and ocelot *Leopardus pardalis* (Linnaeus, 1758)	Giant otter *Pteronura brasiliensis*, Zimmermann 1780
Ranade and Prakash (2015)	Northern red muntjac *Muntiacus vaginalis* (Boddaert, 1785)	Asian elephant *Elephas maximus* Linnaeus, 1758
Laurentino et al. (2019)	White-eared opossum *Didelphis albiventris* Lund 1840 and brown rat *Rattus norvegicus* (Berkenhout, 1769)	Neotropical otter *Lontra longicaudis* (Olfers, 1818)
Fu et al. (2021)	Plateau pika *Ochotona curzoniae* (Hodgson, 1858)	Yak *Bos grunniens* Linnaeus, 1766
Speakman et al. (2021)	Plateau pika *Ochotona curzoniae* (Hodgson, 1858)	Yak *Bos grunniens* Linnaeus, 1766
Gorman (2021)	American pika *Ochotona princeps* (Richardson, 1828)	Yellow-bellied marmot *Marmota flaviventris* (Audubon & Bachman, 1841)
Van der Meer et al. (2022)	Spotted hyena *Crocuta crocuta* (Erxleben, 1777)	African wild dog *Lycaon pictus* (Temminck, 1820)
Waggershauser et al. (2022)	Red fox *Vulpes vulpes* (Linnaeus, 1758)	Domestic dog *Canis lupus* subsp. *familiaris* Linnaeus, 1758
Awasthi et al. (2024)	Northern red muntjac *Muntiacus vaginalis* (Boddaert, 1785), chital *Axis axis* (Erxleben 1777) and wild boar *Sus scrofa* Linnaeus, 1758	Greater one-horned rhino *Rhinoceros unicornis* Linnaeus, 1758
Walton et al. (2024)	Chacma baboon *Papio ursinus* (Kerr, 1792)	Common duiker *Sylvicapra grimmia* (Linnaeus,1758), greater kudu *Tragelaphus strepsiceros* (Pallas,1766), impala *Aepyceros melampus* (Lichtenstein, 1812) and gemsbok *Oryx gazella* (Linnaeus, 1758)

Heterospecific coprophagy may also be motivated by the adult insects or larvae that are developing in the feces (Livingston et al., 2005; Heymann et al., 2011). Other possible functions are the enhancement of the gut flora (Fu et al., 2021) and the removal of scent markers of competitor species (Livingston et al., 2005).

Iberian wild goat *Capra pyrenaica* Schinz, 1838 is a wild Caprinae endemic of steep slope habitats of the Iberian Peninsula (García-González et al., 2020). This species was given the status of Least Concern by International Union for Conservation of Nature (IUCN) and is currently expanding due to natural recovery and reintroductions (Herrero et al., 2021). Iberian wild goats show high feeding plasticity and can exploit different food resources depending on the location and season (García-González and Cuartas, 1992; Martínez, 2009; Moço et al., 2013), but there is only limited understanding of the factors affecting this variation (Acevedo and Cassinello, 2009). In this paper, a case of coprophagy by Iberian wild goats on rock dove *Columba livia* Gmelin, 1789 guano is described, and the potential significance of this behavior is interpreted, based on the nutritional analysis of the guano.

2. Material and methods

The study was conducted in the Guara Natural Park, a protected area with steep calcareous relief, located in the Prepyrenees (Huesca, north-eastern Spain). Relevant characteristics of the area are highlighted in Table 2. On March 14th 2021 at Barranco de la Sosa (42°12′32"N, 0°16′52"W) in Guara Natural Park, one of the authors (EB) observed and filmed two adult female wild goats eating guano in the opening of a cave (Fig. 1; Supplementary videos 1 and 2). The cave is used by rock dove, a colonial and very abundant bird species (the only one with these characteristics that uses it), hence the guano, which formed a 3–5 cm thick layer over the rocky slope, can be confidently assigned to this species. The site was accessed after the animals moved away and two samples were collected from the guano layer at two points about 5 m apart in order to investigate its composition and feed value. Guano samples were sent to laboratory in plastic containers and analyzed for proximate, fiber and mineral composition according to methods of the Association of Official Analytical Chemists International (Latimer Jr, 2019) (Table 3).

3. Results and discussion

3.1. Nutrient composition and feed value

The composition of guano of pigeons and doves has been examined in studies regarding its role in the transmission of zoonotic diseases (Hubalek, 1975; Staib et al., 1978; Chitty et al., 2019), its impact on human constructions (Gómez-Heras et al., 2004; Huang and Lavenburg, 2011; Spennemann and Watson, 2017) and its use as crop fertilizer (Makawi, 1982; Li-Xian et al., 2007). However, little research has investigated this guano as a source of animal feed and only for domestic animals (Nokhtar et al., 1994).

The results of the analysis of the rock dove guano consumed by the Iberian wild goats are given in Table 4. In nutritional terms, its most remarkable feature was the high concentration of nitrogen-compounds (classed together as crude protein), which in pigeon guano consist mainly of uric acid, followed by smaller quantities of xanthine (mostly guanine), urea and creatine (Hubalek, 1975; Staib et al., 1978). These compounds can act as indirect protein sources for ruminants after transformation by rumen microorganisms (Müller, 1980). The levels of crude fat, fiber and nonstructural carbohydrates were low, although the fiber was dominated by labile fractions (hemicellulose > cellulose >

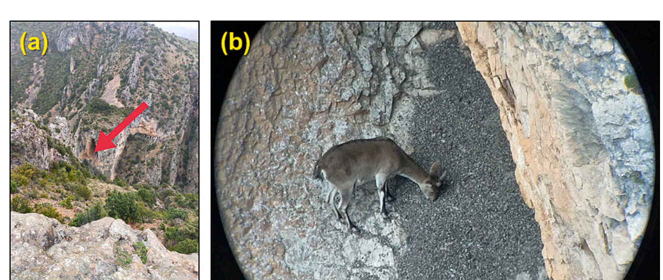

Fig. 1. (a) Location of the cave and (b) a video frame showing an adult female Iberian wild goat eating rock dove guano.

Table 2
Main characteristics of the Guara Natural Park.

Location	42° 16′ 38″ N; 0° 7′ 59 ″ W, on the south flank of the Pyrenees
Extension	40 km *E*-W with an area of 81,494 ha
Altitude	430–2077 m a.s.l.
Geology	Palaeogene limestone, covered on its southern edge with Miocene sandstone and conglomeratic rock
Land cover	About 50% shrubland, 25% forest and 25% rock
Main plant species	
Shrubs	*Echinospartum horridum* (Vahl) Rothm.
	Common juniper *Juniperus communis* L.
	Common box *Buxus sempervirens* L.
Trees (in decreasing order of abundance)	Holm oak *Quercus ilex* L.
	Scots pine *Pinus sylvestris* L.
	Austrian pine *P. nigra* J.F. Arnold.
	Downy oak *Q. cerrioides* Willk. et Costa
	Mountain pine *P. uncinata* Ramond ex A. DC.
	Beech *Fagus sylvatica* L.
Wild ungulates (other than Iberian wild goat *Capra pyrenaica* Schiz, 1838)	
	Wild boar *Sus scrofa* Linnaeus, 1758 (main game animal)
	Roe deer *Capreolus capreolus* (Linnaeus, 1758)
	Red deer *Cervus elaphus* Linnaeus, 1758
	European mouflon *Ovis aries* Linnaeus, 1758
	Fallow deer *Dama dama* (Linnaeus, 1758)
	Feral goat *Capra hircus* Linnaeus, 1758

Table 3
Methods of the Association of Official Analytical Chemists International (AOAC) (Latimer Jr, 2019) and calculations used in the analysis of the dove guano.

	Method
Water	934.01
Crude ash (CA)	942.05
Crude protein (CP)	954.01
Crude fat (ether extract, EE)	920.39
Neutral detergent fiber (NDF)	2002.04
Acid detergent fiber (ADF), acid detergent lignin (ADL)	973.18
Acid detergent ash	928.08
Calcium	962.01
Phosphorus	965.17
Sodium, potassium	956.01
Sulfur	923.01, 973.57
Soluble chloride	943.01
Ammonium, nitrate	920.03, 892.01
Hemicellulose (HEM)	HEM = NDF - ADF
Cellulose (CEL)	CEL = ADF - ADL
Nonstructural carbohydrates (NSC)	NSC = 1000 - [CA + CP + EE + HEM + CEL + ADL] (g/kg)
Total digestible nutrients (TDN) following Weiss (1999)	TDN = 0.98 × NSC + 0.93 × CP + 2.25 × EE −1 + 0.75 × (NDF - ADL) × [1 - (ADL/NDF) x 0.667] – 7

lignin) which contributes to its digestibility (Müller, 1980). The total digestible nutrients content was moderate, meeting the requirements for the maintenance of adult goats (Squires, 2010), but still far from those required for high energy demanding phases such as lactation. The contents of sodium, phosphorus, sulfur and calcium were much higher than their requirements by domestic goats and only potassium among the major minerals was found insufficient (NRC, 2007). On the other hand, phosphorus and calcium exceeded by far the maximum levels tolerable by goats (NRC, 2006), so the excessive consumption of the guano could generate toxic effects. The content of silica (as assessed by acid-detergent ash) was high, possibly derived from contamination by soil or dust, and from the habit of pigeons and doves to ingest soil or gravel particles to help digest grains and seeds (Gómez-Heras et al., 2004).

3.2. Nutritional significance of coprophagy

To our knowledge, the present article provides the first record of heterospecific coprophagy in Iberian wild goat. This feeding behavior has not been observed again by the authors, and it remains to be confirmed whether it extends to more individuals of this species. However, a few reports exist that suggest that bird coprophagy may be a common behavior among *Capra* species. Masseti (2009) documented feral goat *Capra hircus* Linnaeus, 1758 feeding on the excreta of yellow-legged gulls *Larus michahellis* J. F. Naumann, 1840. There is also an indirect report by Hobbs (1989) on Nubian ibex *Capra nubiana* F. Cuvier, 1825 practicing coprophagy on feces of crowned sandgrouse *Pterocles coronatus* Lichtenstein, 1823. Iberian wild goats (Martínez, 2009), as do domestic goats (Allegretti et al., 2012; Mellado, 2016), show a remarkable ability to identify and select in their environment the food resources that best satisfy their specific nutritional needs. The diet of Iberian wild goat in its typical habitats consists mostly of highly-lignified plants with medium-low protein content (Martínez, 2009), which may drive their feeding behavior towards crude protein-rich dove guano. Furthermore, plant forage is subject to regional and seasonal fluctuations in availability and composition, potentially leading to insufficient nutrient supply, especially during high nutrient-demanding periods such as gestation, lactation and growth (Lu, 2011). Indeed, in the same area and time of year, Aldezabal and Garin (2000) observed feral goats turning to alternate forage sources in response to the decrease in nutritive value of the preferred plants during winter. Nutrient shortage has been shown to cause females of various mammal species to lick or eat non-food materials containing such nutrients, e.g. soil (geophagy) or bone (osteophagy), during pregnancy and early stages of lactation (Mori et al., 2018). It is very possible, although it could not be substantiated, that the Iberian wild goat females observed eating guano were pregnant, given that the parturition period of this species in the region starts in late April and peaks in June (Martínez-San Emeterio et al., 2021). Pregnant and lactating females goats search for food low in fiber and rich in crude protein, calcium and phosphorus (Mellado, 2016), both characteristics present in the rock dove guano. Bird coprophagy may also serve as a means to acquire mineral nutrients otherwise not available to goats in the habitat (Masseti, 2009), e.g. phosphorus can be deficient in calcareous areas such as Guara Natural Park (Hejcmanová et al., 2016).

3.3. Hedonistic factors stimulating coprophagy

Dove guano consumption may be stimulated by gustatory factors, especially if the animal experiences a positive post-ingestive effect that feeds back its preference for the food, as has been shown for domestic goats (Provenza, 1995; Papachristou et al., 2005). Goats and other herbivorous mammals show a notable appetite for salty taste, which depends mainly on the concentration of sodium (Ginane et al., 2011; Valentová and Panovská, 2003) but indirectly contributes to the intake of other necessary mineral nutrients (Schulkin, 1991). Taste avidity for sodium can cause wild herbivores, particularly females in the reproductive period, to locate and move long distances to lick soils due to their sodium content (Hebert and McTaggart Cowan, 1971). This may be related to the increased sodium needs during pregnancy and lactation (Schulkin, 1991; Johansson, 2008). The sodium levels of the rock dove guano in our study were about 10–100 times greater than in the soils licked by various wild ruminants examined by Moe (1993) and Ayotte et al. (2006).

Another factor that may contribute to the consumption of dove guano by goats is the occurrence of umami-type flavors. Umami is stimulated by substances such as glutamate or purines derived from the metabolism of protein and nucleic acids (Johnson et al., 2013; Huang et al., 2021) and is used by mammals as a signal of the abundance of nitrogen-components in food (Breslin and Spector, 2008; Favreau et al., 2010). Pigeons' guano is rich in purines, particularly in guanine (Chitty et al., 2019) which is an intense umami flavor enhancer (Huang et al.,

Table 4
Chemical and nutrient composition of the rock dove guano.

	Samples		Values in other studies on pigeons guano					Required	Max. tolerable
g/kg	1	2	A	B	C	D	E		
Water	188	296	446 (283–596)	110	123		429 (201–572)		
Crude ash	310	334		198					
Crude protein	256	246	305 (134–538)	262	277	241			
Crude fat	5.1	4.2		42					
Neutral detergent fiber	386	357							
Acid detergent fiber	204	196							
Acid detergent lignin	70	76							
Acid detergent ash	73	73							
Cellulose	134	120							
Hemicellulose	182	162							
Nonstructural carbohydrates	43	59							
Total digestible nutrients	503	486							
Sodium	10	9						0.5–1.1	40
Phosphorus	13	13			11	16		1.3–3.3	6
Sulfur	5	6				17		2.2–2.6	5
Potassium	0.4	0.4			19	39		4–7	20
Calcium	35	37				32		1.4–6.0	15
Chloride	< 0.5	< 0.5			6	15		2	
Ammonium-nitrogen	2.9	2.2					34 (32–35)		
Nitrate-nitrogen	1.5	1.1							2

All values are expressed as g per kg ash-free dry matter basis except water is expressed in g per kg fresh matter.
Reference values: A = Mean (minimum and maximum) reported by Hubalek (1975), B = Nokhtar et al. (1994), C = Li-Xian et al. (2007), D = Huang and Lavenburg (2011), E = Mean, minimum and maximum compiled by Spennemann and Watson (2017). Required values and maximum (max.) tolerable values are those given by NRC (2006, 2007), respectively.

2021). Ruminants show a strong preference for umami flavored food (Ginane et al., 2011), especially when it is protein-rich (Favreau et al., 2010). Guanine may favor the guano consumption by goats, and this behavior be reinforced post-ingestion by the positive effect of the intake of nitrogen-compounds convertible into protein. This effect could be especially marked in females at the second half of their gestation period, when the protein requirements markedly increase (Squires, 2010; Haydarov et al., 2020).

3.4. *Exposure effects and pathogenicity*

Before being consumed, the rock dove guano had been exposed to air and sunlight for an undetermined time. Exposure effects included desiccation as can be seen from the water contents (Table 4), which were on the low end of the ranges reported for pigeon guano by Hubalek (1975) and Spennemann and Watson (2017), but above the values of the guano fully dried by sun or air reported by Nokhtar et al. (1994) and Li-Xian et al. (2007). Exposure may be also responsible for the low levels of highly mobile elements such as chloride or potassium as result of the intense leaching that dove guano experiences when it is exposed outdoor (Gómez-Heras et al., 2004). Guano aging also associates with microbial nitrification (Spennemann and Watson, 2017), which was evident here in the low ammonium content and significant presence of nitrate.

Outdoor exposure, in particular the degree of insolation, can be crucial for this feeding habit because they can affect the pathogenicity of guano. Pigeon and dove droppings are long reported (e.g. Hubalek, 1975; Staib et al., 1978) as a major reservoir of *Cryptococcus neoformans* (San Felice) Vuill. 1901, a fungus able to grow on uric acid and creatinine as nitrogen sources. *C. neoformans* is the main causative agent of cryptococcosis, a potentially lethal zoonotic disease affecting a wide variety of domestic and wild animals (Danesi et al., 2021; Bermann et al., 2023). Cryptococcosis is occasionally reported in domestic goats, in which it develops as pulmonary, neurological and skin disease (Do Carmo et al., 2020; Sharma and Rana, 2023). It also occurs in mouflons *Ovis aries* Linnaeus, 1758 (Maestrale et al., 2015) and possibly other species of wild Caprinae, but its incidence in Iberian wild goat is unknown. Infection by *C. neoformans* in goats usually occurs through inhalation of spores from the environment (Do Carmo et al., 2020), but may also occur through the ingestion of desiccated fungal cells (Sharma and Rana, 2023). For example, goats have been suggested to acquire *C. neoformans* by eating the bark of certain trees containing the fungus (Cogliati et al., 2016). *C. neoformans* is tolerant to desiccation and can survive in the guano for up to 20 years in dark, humid sheltered sites (Pal and Dave, 2016), but is sensitive to ultraviolet light and is generally absent from the guano in open, sun-irradiated sites (Hubalek, 1975; Abbas et al., 2010) such as that we studied. Exposure to direct sunlight for a period of three weeks is reported to be sufficient to neutralize the pathogenicity of pigeon guano and allow it to be safely consumed by animals (Nokhtar et al., 1994).

4. Conclusions

Heterospecific coprophagy is reported for the first time for Iberian wild goat. Adult females of this species were observed eating rock dove guano. The guano consumed by the goats was largely dry and depleted in soluble and volatile components as result of outdoor exposure, which might have also decreased its pathogenicity. In nutritional terms, the dove guano has a high content of nitrogen-components, particularly of uric acid, which can be used by ruminants for their protein nutrition. It is also rich in major nutrients such as sodium, phosphorus, sulfur and calcium, so that its consumption may contribute to alleviate deficiencies in these elements. Hedonistic factors such as the saltiness from sodium and umami taste from guanine might play a role in stimulating its consumption. We hypothesize that female Iberian wild goats could be stimulated by guano in the second half of their pregnancy period, when their protein requirements are larger. Heterospecific coprophagy has been documented in a wide range of mammal types indicating it may be an important feeding activity, but it is still poorly studied and understood. Its reason, consequences and relevance should deserve more attention to better understand their feeding ecology. This has to be faced under a multidisciplinary approach.

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CRediT authorship contribution statement

Juan Luis Mora: Conceptualization, Investigation, Writing – original draft, Writing – review & editing. **Enrique Blasco:**

Conceptualization, Investigation, Writing – review & editing. **Alicia García-Serrano:** Conceptualization, Investigation, Writing – review & editing. **Juan Herrero:** Conceptualization, Investigation, Writing – review & editing.

Declaration of generative AI and AI-assisted technologies in the writing process

None.

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.

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