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Animal-fungal interactions 3: first report of mycophagy by the African Brush-tailed Porcupine *Atherurus africanus* Gray, 1842 (Mammalia: Rodentia: Hystricidae)

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Mycophagy is a widespread phenomenon across many groups of mammals, birds, and reptiles around the world (Fogel & Trappe 1978; Claridge & May 1994; Cooper & Vernes 2011; Elliott & Vernes 2019). The behaviour is well-documented in some groups of animals while largely overlooked in others. The African continent has an incredible diversity of mammals; however, the majority have not been studied to determine if fungi are an important part of their diets. Most reports of mycophagy in Africa are of primates (Bermejo et al. 1994; Isbell 1998; Fossey 2000; Hanson et al. 2003; Isbell & Young 2007; Georgiev et al. 2011). There are scattered reports of mycophagy by non-primate vertebrates in Africa including six species of the African tortoise genus *Kinixys* (Hailey et al. 1997), the Suni *Neotragus moschatus* (Heinichen 1972), the Bushbuck *Tragelaphus scriptus* (Odendaal 1977, 1983), and Brown Hyaena *Hyaena brunnea* (Mills 1978). Since many of the fungi that are consumed by animals are mycorrhizal, the dispersal of spores assists with overall forest health and symbiotic colonization of plant roots (Cázares & Trappe 1994; Colgan & Claridge 2002; Caldwell et al. 2005; Trappe & Claridge 2005; Elliott et al. 2018). Fungi are typically very nutritious, making them important to many animals diets (Vogt et al. 1981; Cork & Kenagy 1989; Hussain & Al-Ruqaie 1999; Claridge & Trappe 2005; Kalač 2009; Wallis et al. 2012).

The African continent has more than 2,000 described macrofungi and is estimated to have twice that many undescribed species (Schmit & Mueller 2007). Given the prevalence of mycophagy in other regions of the world and the high diversity of African animals and fungi, it is very likely that similar relationships evolved, but were not studied. In this paper, we provide the first report of mycophagy by the African Brush-tailed Porcupine *Atherurus africanus*.

In September 2014, while conducting mycologic studies of ectomycorrhizal fungi near the village of Somalomo, Cameroon (3.358^{0}N & 12.729^{0}W, 650m), we

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found that villagers were conducting some trapping in the area outside of the Dja Biosphere Reserve. We expressed interest to local hunters to have access to samples of stomach contents of any animals that they might have already killed. We were provided with the stomach contents of an African Brush-tailed Porcupine (Image 1A). The hunter asked to remain anonymous.

When the stomach contents were first examined macroscopically, we observed what appeared to be numerous pieces of the exterior of the hypogeous fungus genus *Elaphomyces* Nees (Eurotiales, Ascomycota). The stomach contents were stored in alcohol and were thoroughly mixed; four slide mounts were then made in water and examined with a Zeiss light microscope at 400x and 1000x magnification. Visual scanning of the stomach contents showed high densities of fungal spores (approximately 60–80 % of visible material). Spores were globose, dark brown between 35–40 µm in diameter (including ornamentation), with prominent, reticulate-alveolate ornamentation up to 4.5µm tall (Image 1C,D). These spores matched the species *Elaphomyces favosus* Castellano & T.W. Henkel that was first collected and described approximately 5km away from where the porcupine was trapped (Image 1B; Castellano et al. 2016a). Image 1B shows collection: Henkel 9874 (YA, HSC G1175, OSC 149786, K(M) 200224); GenBank accession numbers: ITS KT694135; 28S KT694147 (see the full technical description of this collection and species, in Castellano et al. 2016b). We were unable to find any other spore types present in the sample.

This is the first report of mycophagy by an African Brush-tailed Porcupine and the first report of mycophagy of the genus *Elaphomyces* in Africa. The genus *Elaphomyces* is widely eaten by animals, ranging from rodents and wild boar to marsupials, but it was never reported as a food source in Africa (Boudier 1876; Fogel & Trappe 1978; Vogt et al. 1981; Genov 1982; Cork & Kenagy 1989; Vernes et al. 2001, 2004; Vernes & Poirier

Image 1. A - The trapped African Brush-tailed Porcupine *Atherurus africanus* from which we sampled the stomach contents for our study; B - Fruiting bodies of *Elaphomyces favosus* (collection number Henkel 9874) collected from near the locations where the porcupine was trapped. The spores of this collection match those found in the stomach contents, indicating that the porcupine was digging and eating this species; C - A microscope mount at 40x magnification of stomach contents showing the density of spores typically observed; D - A spore of *E. favosus* at 1000x magnification from the stomach sample of the porcupine. © Todd F. Elliott

2007; Nuske et al. 2017b). We provide evidence from one sample, but based on studies of mycophagy in other parts of the world (Fogel & Trappe 1978), this likely represents a common but understudied behaviour among many African mammals. To our knowledge, only three other studies from Africa reported sequestrate (truffle-like) fungi being consumed by mammals; two involved unidentified "truffle" species being eaten by Bonobos *Pan paniscus* (Bermejo et al. 1994; Georgiev et al. 2011), and one involved *Kalaharituber pfeilii* (published as *Terfezia pfeilii*) being eaten by Brown Hyaena *Hyaena brunnea* (Mills 1978). In native and non-native forest habitats across sub-Saharan Africa, at least 15 species of sequestrate fungi from nine families have been reported (Dissing & Lange 1962; Dring & Pegler 1978; Castellano et al. 2000, 2016a,b; Ferdman et al. 2005; Beenken et al. 2016). These fungi likely evolved associations with vertebrates to enhance their spore dispersal and, in turn, may be an important component of these animals' diets (Cázares & Trappe 1994; Beenken et al. 2016). Ori et al. (2018) found that Crested Porcupines *Hystrix cristata* ate the sequestrate fungus *Tuber aestivum* in Italy and that some spores germinated in the scats, indicating that the mycorrhizal fungal spores are viable after passage through porcupine digestive tracts. We suspect spores would be similarly viable after passage through *Atherurus africanus* digestive systems.

The ectomycorrhizal fungal genus *Elaphomyces* forms a mutualistic symbiosis with the roots of a broad range of angiosperm and gymnosperm hosts in temperate and tropical regions (Trappe et al. 2009; Castellano et al. 2011, 2012, 2018; Paz et al. 2017). In tropical Africa, *Elaphomyces* was found in association with the tropical ectomycorrhizal tree *Gilbertiodendron dewevrei* (Castellano et al. 2016a). Ectomycorrhizal fungi play critical roles in host plant nutrition by mobilizing essential nutrients to their hosts in exchange for a carbon source (Smith & Read 2008). Their roles in tree establishment and survival directly influence species composition and the dynamics of plant communities (Peay et al. 2008; Tedersoo et al. 2010). Ectomycorrhizal fungi in tropical regions are thought to facilitate monodominance of ectomycorrhizal trees in forest regions otherwise composed of a wide diversity of tree species, which could also be the case for *G. dewevrei* (Henkel 2003; Peh et al. 2011; Corrales et al. 2016). *Elaphomyces* species and similar sequestrate fungi rely primarily on animal consumption for dispersal, and these mycophagists (eaters of fungi) are therefore essential to the maintenance of this fungal diversity, plant-fungal relationships, and related functions in the ecosystem (Nuske et al. 2017a). Maintaining both mammal and fungal diversity may, therefore, be essential in the management and conservation of these forest ecosystems, and we urge for further studies on the importance of mycophagy in Africa.

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