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Review Papers

Aves and Fungi interactions in a review of mycophagy and its associations in wildlife and industry

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Abstract
Fungi and Aves are present in all ecosystems and interact with a variety of organisms. The purpose of this study was to compile and analyze in the literature the mycophagy and association of birds with fungi to evaluate the aspects of interaction habits and habitat in natural and industrial environments. In this study, 64 species of wild birds were found with documented interactions involving fungi. However, only 32 had the consumed or used-for-nesting fungi species fully identified. In these cases, there is a correlation between the birds' foraging habits and the habitats of fungi. According to the findings of this review study, birds' foraging habits are closely linked to fungi habitats in relation the interactions between the groups. Also, the poultry industry is increasingly using mushrooms as a nutritional supplement due to their benefits. Despite the limited knowledge about the nutritional benefits of these associations in the wild, results from the industry indicate that the benefits would be similar.
Key words: avian mycophagy, beneficial associations, foraging habits, natural and artificial food, poultry farming.

Resumo
Fungos e aves estão presentes em todos os ecossistemas, interagindo com uma variedade de organismos. Este estudo teve como objetivo compilar dados na literatura sobre a micofagia e analisar as associações das aves com fungos, avaliando os aspectos de hábitos e habitats nos ambientes naturais e industriais. Neste estudo, foram encontradas 64 espécies de aves silvestres com interações documentadas envolvendo fungos. No entanto, apenas 32 tiveram as espécies de fungos consumidas ou usadas para nidificação completamente identificadas. Nestes casos, há uma correlação entre os hábitos de forrageamento das aves e os habitats dos fungos. De acordo com os resultados desta revisão, os hábitos de forrageamento das aves estão intimamente ligados aos habitats dos fungos em relação às interações entre os grupos. Além disso, a indústria avícola está utilizando cada vez mais cogumelos como suplemento nutricional devido aos seus benefícios. Apesar do conhecimento limitado sobre os benefícios nutricionais dessas associações na natureza, os resultados da indústria indicam que os benefícios podem ser similares.
Palavras-chave: micofagia aviária, associações benéficas, hábitos de forrageamento, alimentação natural e artificial, avicultura.

See supplementary material at <10.6084/m9.figshare.26008204>

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Introduction

There are approximately 3.8 million species of fungi that have been cataloged (Hyde *et al*. 2020), with the first appearing 1.2 billion years ago (Berbee & Taylor 2010). Fungi can be found in various ecosystems, including aquatic, terrestrial, and arboreal environments, and they interact with a wide range of organisms, including mammals, arthropods, birds, and plants (Tiquia-Arashiro *et al*. 2019). It is estimated that birds originated approximately 95 million years ago (Lee *et al*. 2014) and currently encompass a total of 10,426 recorded species (Gill *et al*. 2022). Similar to fungi, they have been found in all ecosystems, exhibiting a range of feeding habits from specialists to generalists (Ericson *et al*. 2006). Birds employ various foraging tactics, including aerial, terrestrial, and aquatic environments (Robinson & Holmes 1982). This diversity is further categorized into three main groups: carnivores, herbivores, and omnivores (Beddall 1957).

Several characteristics of fungi, such as shape, size, color, aroma, and texture, contribute to the interaction between prey and predator in mycophagy (Beever & Lebel 2014). Fungal spores can be dispersed through interactions with fauna, consumption, internal or external travel with consumers or travelers, and defecation (O'Malley *et al*. 2013; Horton 2017; Jusino *et al*. 2022). According to Costa *et al*. (2022), *Molothrus bonariensis* (Gmelin 1788) acts as a dispersing agent of *Macrolepiota bonariensis* in the studied area through mycophagy activities and subsequent defecation.

Many fungi disperse their spores by wind (Golan & Pringle 2017), but most distances considered within reach are minimal, with up to 95% of the spores remaining within one meter of the fungus (Galante *et al*. 2011; Horton *et al*. 2013). Elliott & Vernes (2019) reported a relationship between fungal habitat and the foraging habits of birds. This relationship was observed in the case of *Menura novaehollandiae* (Latham 1801), which feeds on *Rossbeevera vittatispora*, a soil fungi. Other forms of association between birds and fungi exist in relation to habitat and foraging behavior. For instance, *Colaptes auratus* (Linnaeus 1758) has been documented interacting with *Fomes fomentarius*, where did the bird show a preference for excavating nests in trees with the presence of the fungi (Martin *et al*. 2004; Edworthy *et al*. 2012; Lorenz *et al*. 2015).

According to Elliott *et al*. (2019), avian mycophagy is more widespread than previously believed. Caiafa *et al*. (2021) demonstrated that several truffle species in Patagonia rely partially on birds for their dispersal, including *Scelorchilus rubecula* (Kittlitz 1830) and *Pteroptochos tarnii* (King 1831). However, numerous unanswered questions persist regarding the evolution of mycophagy in birds, the significance of feeding habits in their natural environment, and the correlation between avian feeding and foraging behaviors in relation to fungal habitats. Furthermore, limited knowledge exists regarding the nutritional value of fungi in the diets of birds.

Nutritional supplementation with fungi in poultry farming has been found to be beneficial (Azevedo & Barata 2018). Studies involving broiler chickens (*Gallus gallus* - Linnaeus 1758) have shown that the inclusion of fungi in feed improves the nutritional quality of meat, intestinal microbiota, immune responses, and antioxidant activity (Bidarnamani *et al*. 2015; Bederska-Lojewska *et al*. 2017; Mahfuz *et al*. 2020; Lima *et al*. 2021). Similar results have also been observed in other types of meat industries, such as duck, goose, quail, and turkey (Bederska-Lojewska *et al*. 2017).

Regardless of whether birds ingest fungi naturally or artificially in the industry, mycophagy occurs. There are few studies that demonstrate the interactions, nutritional benefits, behavior, and foraging of birds that include fungi in their diet. The study aims to compile and analyze literature data on the mycophagy of birds to investigate the habit and habitat aspects of this interaction. Furthermore, it aims to compile the benefits associated with including fungi in poultry industry diets.

Material and Methods

Bibliographic survey

A bibliographic review was conducted on bird and fungi species involved in mycophagy, which have been published in scientific articles, reports, book citations, and digital public platforms such as Web of Science (<https://www.webofscience.com>) and Google Scholar (<https://scholar.google.com>). The keywords "aves", "birds", "fungi", "mushroom", "mycophagy", "fungivory", and "poultry farming" were utilized. Data pertaining to interactions and food in natural or industrial environments were collected. This study cites information from the literature that involves identified or unidentified species, as well as fungi taxonomic groups.

Statistical analysis of the foraging habits and fungi habitat

A file in Excel format (Walkenbach 2010) containing binary data was compiled to analyze the foraging habits of birds and fungi habitats. The graphs were elaborated using the R v.3.6 program (Ihaka & Gentleman 1996) and presented in percentage values (habitat/habit). Birds were classified as terrestrial or arboreal foragers (Gill *et al*. 2022), and the fungi were designated as terrestrial for those growing on soil, and arboreal for those growing on wood (Putzke & Putzke 2017, 2019).

Foraging habit and habitat characteristics were categorized into four categories: Partial Foraging on Ground (PFG); Major Ground Foraging (MGF); Partial Arboreal Foraging (PAF); and Major Arboreal Foraging (MAF). In addition, two positions were tested: Predominant Vertical Position (PVP) and Predominant Horizontal Position (PHP). Two categories of fungi were tested according to their habitat: Terrestrial Habitat (TH) and Arboreal Habitat (AH). The characteristics of species and the percentages were calculated in the model by Fávero & Belfiore (2017).

Results and Discussion

Records of the interaction between birds and fungi in the literature

This bibliographic review study found reports of 64 bird species interacting with fungi in the wild. However, only 32 birds had the consumed fungi species fully identified. A total of 29 families belonging to Bucerotiformes, Casuariformes, Charadriiformes, Dinornithiformes, Galliformes, Passeriformes, Piciformes, Psittaciformes and Trogoniformes were cataloged (Tab. S1, available on supplementary material <10.6084/m9.figshare.26008204>). In the literature, the consumption of fungi by birds is commonly described in imprecise ways, not identifying the fungi species involved. Regarding the fungi, only 32 species belonging to 17 families of Cyttariales, Pezizales, Polyporales, Hymenochaetales, Russulales, Boletales, and Agaricales were identified (Tab. S1, available on supplementary material <10.6084/m9.figshare.26008204>).

Many incomplete instances of associations between birds and fungi have been documented in the literature. In Table S1 (available on supplementary material <10.6084/m9.figshare.26008204>), fungi that were not properly identified are classified according to class, order, family, and genus. Despite the need for further evidence to refute or support these claims, it is important to cite them as they provide a foundation for future studies. Additionally, taxonomic identification of fungi can be challenging due to their complexity. Moreover, many cited reports refer to observations made by ornithologists or naturalists regarding feeding behavior or the utilization of fungi as a resource, particularly in relation to nest excavation.

Observational reports comprise the majority of studies on the interaction between birds and fungi. In relation the mycophagy, many reports in the literature describe birds foraging near the presence of fungi. As for nest excavation, the birds are reported using trees with fungi present. The studies that involved DNA sampling and gastrointestinal analysis were not specifically conducted to investigate mycophagy, although they were mentioned due to the significance of the results. The study of this interaction generally requires collaboration because many reports involving birds do not correctly identify the fungi involved. It is difficult to understand how the Aves-Fungi interaction occurs when the fungi are not identified. Which fungi species are consumed by birds, or which fungi are involved in the nest excavation process, for example, remain unclear.

Birds foraging behavior and its fungal associations

A summary of the main relationships between birds' foraging habits and fungi habitats for the identified species is shown in Figure 1. The foraging and mycophagy habits of birds indicate that species of the orders Galliformes and Bucerotiformes consume terrestrial fungi during foraging. The horizontal position on the ground during foraging is predominant in Galliformes, as reported by Schutz *et al*. (2001) and Trupkiewicz *et al*. (2018). In this group, *Gallus gallus* has reportes in mycophagy with *Armillaria gallica*, *Entoloma abortivum*, and *Hypholoma lateritium* (Elliott & Vernes 2019). *Laccocephalum mylittae* has also been associated with Malleefowl (*Leipoa ocellata*), and *Lentinula lateritia* has been found in the diet of Australian brushturkey (*Alectura lathami*) (Benshemesh 1992; Reichelt & May 1997; Simpson 1998, 2000). It is important to emphasize that all the mushrooms mentioned above are edible and grow in soil (Miller & Miller 2006), and that the birds are ground foragers.

Most studied Passeriformes consume terrestrial fungi as part of their diet, with a small proportion consuming arboreal fungi. According to Martin (2017), Passeriformes adopt both horizontal and vertical foraging positions, and their habits are highly diverse. *Agaricus campestris* is an edible species that grows in the ground (Putzke & Putzke 2017) and has been associated with the mycophagy behavior of *Corvus brachyrhynchos*, a bird that forages in the soil (Webster 1902; Kilpatrick 2003). Additionally, *Cormobates leucophaea* is an arboreal forager that primarily forages vertically (Christidis *et al.* 2008). The species was reported in mycophagy with *Laetiporus portentosus* (Maurer *et al*. 2017), an edible medicinal mushroom that grows on wood (Fuller *et al.* 2005).

The Psittaciformes are primarily insectivorous and frugivorous, adopting a wide variety of foraging positions. *Alisterus scapularis*, for example, has been observed in a horizontal position during foraging (Plant *et al*. 2020). There have been records of this bird feeding on *Cyttaria gunnii* (Elliott & Elliot 2019), which forms globose structures on the branches of the host tree resembling fruit silhouettes. These structures are also edible and orange in color (Leonard 2017). *Trogon surrucura* (Trogoniforme) is both a frugivore and an insectivore with extensive foraging abilities, both terrestrially and arboreally, in a variety of vertical and horizontal positions (Sarquis *et al*. 2017). Birds of this species has been reported feeding on *Fomes fasciatus*, a fungus that grows on tree trunks (Cockle *et al*. 2012).

To Jusino *et al*. (2015), Piciformes, especially woodpeckers, prefer to excavate trees infected with lignicolous fungi because the excavated material is easily accessible. The compounds lignin and cellulose confer greater resistance to the cell wall of plants, but they are degraded by fungi. The "Tree Selection Theory" proposes that woodpeckers prefer these trees due to the ease of excavation (Jusino *et al*. 2015). During the study conducted with *Picoides borealis*, over 50

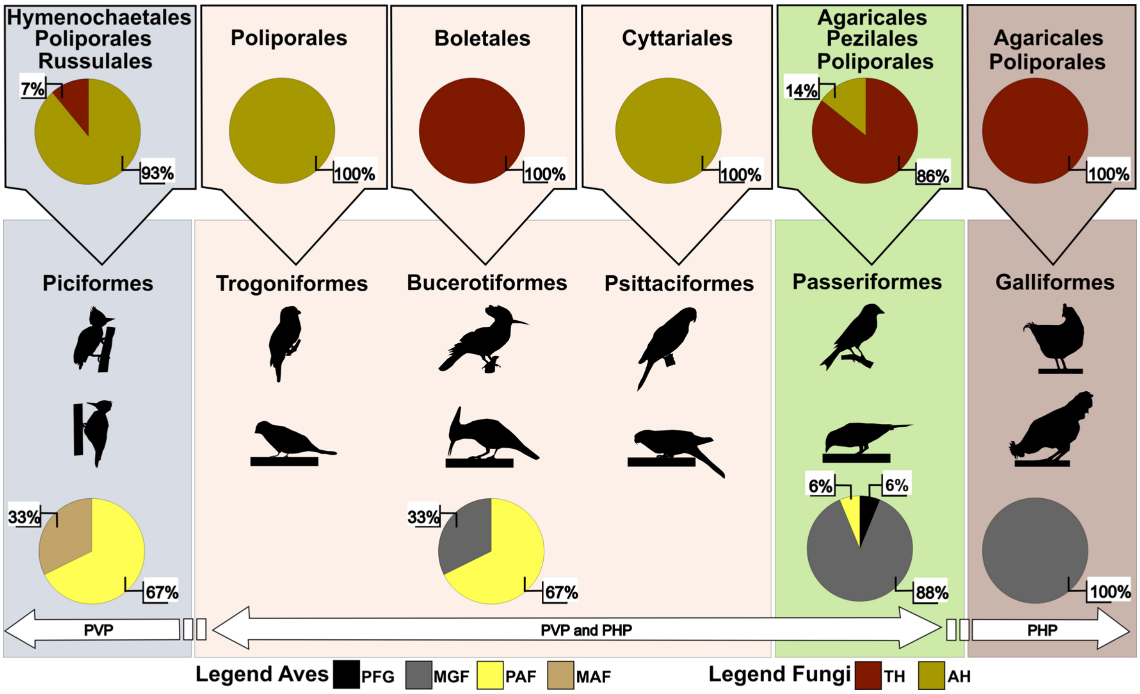

Figure 1 – Interactions of birds with fungi. The pizza graphs show the percentages for each listed category and the silhouettes of the birds are represented according to the species in this study. The arrows indicate the trend of horizontal or vertical position during foraging. PVP = predominant vertical position; PHP = predominant horizontal position. Legends Aves: PFG = partial foraging in ground; MGF = major ground foraging; PAF = partial arboreal foraging; MAF = major arboreal foraging. Legends Fungi: TH = terrestrial habitat; AH = arboreal habitat. * = Picidae (Piciformes) with fungal associations detected in the nests of birds. Source: Authors (2023).

species of fungi were associated with the bird's preference for choosing trees to excavate (Jusino *et al*. 2016). However, there is a gap to be filled in relation to mycophagy involving woody fungi in particular within this bird's group. Despite this, it is important to mention a correlation to a preference for excavating nests in places where wood fungus occurs. In the future, this group could be further analyzed regarding the presence or absence of mycophagy activities. However, it is reasonable to infer that they act as dispersal agents since they coexist with the sites where wood fungi are present.

There is a wide variety of behaviors that birds may display during their foraging activities, which can be characterized as opportunistic, incidental, or even compulsory interactions with food sources. Various strategies can be employed, including considering the characteristics of prey biomass (LeBrasseur 1969), the ease of capturing or manipulating prey, the duration of foraging, as well as the presence of predators or competitors during the activity (Brink & Dean 1966). In this regard, one of the advantages of including fungi in birds' diets is the lack of an escape response by the prey (Samson *et al*. 2019). The literature does not describe the specific strategies used for mycophagy, which poses an important question for future research. However, our data collection provides evidence that arboreal foragers consume fungi from the same habitat/substrate, or have some form of association with them, such as when they excavate nests. Conversely, terrestrial foragers tend to include or interact with soil fungi.

Optimal Foraging Theory explains that diet follows certain concepts: I) The occurrence of predators is independent of the abundance of prey; II) The predator may not specialize in unprofitable prey; III) There is not take of food by partial preference; IV) Encounter and capture rates are sequential, and not simultaneous (Helfman 1990). Homogeneous environments in food distribution are rare while heterogeneous environments generally predominate. In order to be effective foragers, species must establish a favorable cost-benefit relationship (Adamík *et al.* 2003). Based on these results, further exploration of bird mycophagy should be undertaken in the future. It is worth noting that Galliformes do not forage in trees but may roost in them. Passeriformes adopt an intermediate position during foraging, often perching pointed downward constantly. Piciformes, Psittaciformes, Bucerotiformes, and Trogoniformes spend most of their time perched but also feed on the ground.

The use of mushrooms in poultry farming

The results of studies on the feeding efficiency of mushrooms in broiler chickens are presented in Table S2 (available on supplementary material <10.6084/m9.figshare.26008204>). There are some species of mushrooms that are consumed more frequently, such as *Agaricus bisporus*, also known as champignons. Due to its nutritional value, insects, reptiles, birds, mammals and humans consume this species (Azevedo & Barata 2018). Increasingly, mushrooms are becoming popular not only for their nutritional value but also as nutraceuticals used in the meat industry, particularly in poultry (Bederska-Lojewska *et al*. 2017). Studies have shown that mushrooms have a positive effect on feeding, resulting in increased body mass and improved meat quality (Camay 2016; Yan *et al*. 2018; Ilyina *et al*. 2020).

Studies in aviculture indicate promising results when fungi are added to diets. In natural environments, species of fungi that have been reported in mycophagy with birds, as well as with other taxonomic groups, are included in the poultry industry's diet (Azevedo & Barata 2018). For example, *Agaricus* has been reported as food in mycophagy by birds of the Corvidae and Muscicapidae families (Tab. S1, available on supplementary material <10.6084/m9.figshare.26008204>). In the industry, the same genus is used to feed Phasianidae and Anatidae (Tab. S2, available on supplementary material <10.6084/m9.figshare.26008204>). Clearly, these avian groups have a significant commercial interest, but *Agaricus* also has associations of mycophagy with other birds in the wild. Unpublished studies have demonstrated the nutritional and immunological benefits of consuming fungal species that are already classified as edible in the diets of avian species (Guo *et al*. 2004; Camay 2016; Mahfuz *et al*. 2020). These results can naturally occur in mycophagy associations of wild birds.

Poultry farming is constantly confronted with the use of antibiotics for bacteria control (Camay 2016). Recent studies have shown an increased use of fungi in pathogen control in recent years, as avian species develop resistance to drugs (Mahfuz *et al*. 2020). An example of this argument is the study by Guo *et al*. (2004), which used extracts of *Lentinula edodes* and *Tremella fuciformis* to control bacterial infection caused by the pathogen *Mycoplasma gallisepticum* in broilers. An effect similar to the antibiotic Apramycin was observed, along with a benefit to intestinal flora when the extract of these fungi was used (Guo *et al*. 2004) (Tab. S2, available on supplementary material <10.6084/m9.figshare.26008204>). There has been a description of *Alectura lathami* engaging in mycophagy with *Lentinula lateritia* (Simpson 1998, 2000), a fungus of the same genus, but in the wild (Tab. S1, available on supplementary material <10.6084/m9.figshare.26008204>). Although *Tremella fuciformis* is not associated with mycophagy in wild birds, it is an edible species (Stamets 2000).

In studies with broilers, diets supplemented with *Pleurotus ostreatus*, *Agaricus bisporus*, *Flammulina velutipes*, and *Lentinula edodes* showed health benefits (Tab. S2, available on supplementary material <10.6084/m9.figshare.26008204>). Supplementation resulted in improvements in growth, better meat quality, and a reduction in bacterial infections (Camay 2016; Mahfuz *et al*. 2020). Additionally, the inclusion of fungal supplements in broiler feed led to a significant decline in *Escherichia coli* infections in the group with the supplemented diet (Shang *et al*. 2014). In the study by Hines *et al*. (2013), supplementation with mushrooms also led to an increase in the populations of *Lactobacillus* spp. and *Bifidobacterium* spp. which are beneficial to the intestinal tract.

The inclusion of *Agaricus blazei* as a powdered extract in broiler feed resulted in significant reductions in serum cholesterol levels (Fanhani *et al*. 2016). Additionally, the addition of *Pleurotus ostreatus* to broiler diets significantly decreased serum triglyceride concentrations (Toghyani *et al*. 2012). In this premise, Kavyani *et al*. (2012) reported an increase in antibody production in the blood cells of chickens fed these mushrooms compared to the control group. Birds naturally consume mushrooms of this genus during foraging activities (Tab. S1, available on supplementary material <10.6084/m9.figshare.26008204>). However, the benefits associated with mycophagy have been studied primarily in the avian industry, but they can also occur in nature.

In poultry farming, the study is also exploring the use of fungi diets in other species, such as ducks (*Anser anser*), geese (*Cairina moschata*), quail (*Coturnix coturnix*), and turkeys (*Meleagris gallopavo*). The results of fungi supplementation in these groups are presented in Table S2 (available on supplementary material <10.6084/m9.figshare.26008204>). In general, both the fungal and avian industries are developing products which can provide low-cost feed and better nutritional value (Bederska-Lojewska *et al*. 2017).

The main benefits associated with the inclusion of fungi in poultry farming are improved nutritional retention, enhanced performance of the intestinal tract, and increased production of antibodies. There are variations in physiological responses among poultry species due to the diversity and composition of mushrooms in their diets. Further research is crucial to investigate dosage, preparation methods, and the inclusion of new fungal species in avian diets. Currently, there are only study results demonstrating how avians respond nutritionally to the inclusion of fungi in their diet. Considering that mycophagy occurs naturally, these studies could serve as a foundation for future research.

The association of birds with fungi in their diet or interactions, such as nest building, is important for natural ecosystems and should be further explored in the future. Numerous benefits have been mentioned regarding the inclusion of mushrooms in poultry farming, which can also be applicable for studying wild species based on their potential. There are several unidentified species of fungi reported in these associations, and inaccurate reports should be reviewed in the future. Conversely, research in the poultry industry has demonstrated the advantages of supplementing avian diets with fungi.

Considering the presence of fungi in all ecosystems, especially before the emergence of birds, suggests that mycophagy may have been very ancient. Additionally, the foraging behavior of birds should be analyzed in relation to the occurrence of fungi to gain a deeper understanding of the correlation. Several intrinsic and extrinsic factors may contribute to a better understanding of the interaction between birds and fungi in feeding. Avian associations with mycophagy represent an emerging field, and this review can serve as a foundation for further studies in this area.

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Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

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