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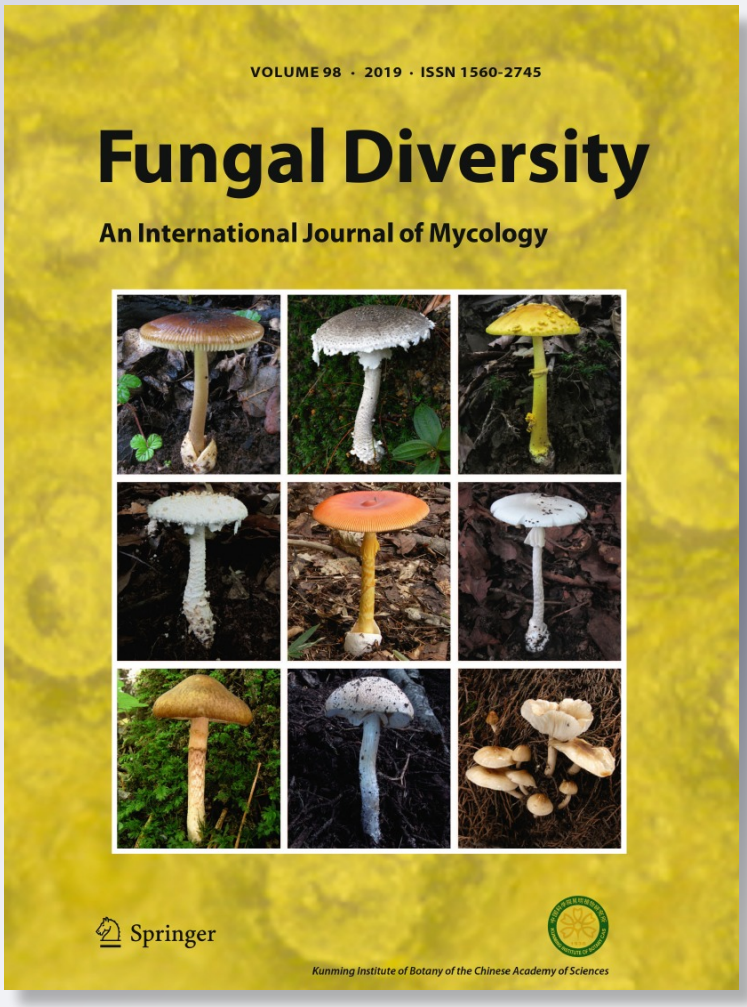


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REVIEW

# A global review of the ecological significance of symbiotic associations between birds and fungi

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## Abstract

Symbiotic associations between mammals and fungi have been well documented and are widely regarded as vital to ecosystem functions around the world. Symbioses between birds and fungi are also ecologically vital but have been far less thoroughly studied. This manuscript is the first to review a wide range of symbiotic associations between birds and fungi. We compile the largest list to date of bird species reported to eat fungi (54 bird species in 27 families) and follow up with a discussion of these symbioses and suggestions for how future studies can determine the prevalence of associations between birds and fungi. We review the importance of fungi for cavity-excavating birds and show that at least 30 bird species in three families form varying levels of associations with fungi for cavity excavation. We also review the use of fungal rhizomorphs in nest construction and show that 176 bird species in 37 families use fungal material in their nests. All of these interactions have wide-reaching ecosystem implications, particularly in regard to fungal dispersal and biogeography, plant health, ecosystem function, bird nutrition/fitness and bird behaviour.

**Keywords** Mycorrhizae · Fungal dispersal · Ornithomycological associations · Bird nutrition · Mycophagy · Rhizomorphs · Cavity-nesting · Tree hollows

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## Introduction

Birds and fungi fill diverse ecological roles around the world. There are many peer-reviewed publications, popular articles and field guides generated each year by mycologists and ornithologists about their respective fields and numerous professional and amateur organisations dedicated to these groups of organisms. Despite the substantial public and scientific interest in these groups, surprisingly little research has focused on ornithomycological (bird-fungal) interactions and the possible coevolution of birds and fungi. We argue that this area of research—though insufficiently studied—is important for both mycology and ornithology, as well as the broader scope of ecology.

Representatives of the fungal kingdom are present in virtually every ecosystem; the prevalence of fungi effectively leads to their direct or indirect interaction with all other organisms. These interactions range from generalist to specialist and from parasitic to mutualistic (Peay et al. 2008). Fungi have effective enzymatic abilities that allow them to extract nutrients from many biotic and abiotic

materials (Peay et al. 2008). These enzymatic capabilities enable nutrient cycling that has a ripple effect throughout ecosystems (Smith and Read 2008). For example, roots of the majority of plants form mycorrhizal associations with fungi that facilitate the uptake of nutrients and water from soil; in exchange, sugars produced by the plants' photosynthesis are transferred to the fungi (Trappe 1962; Tedersoo et al. 2010). Other groups of fungi are key to the breakdown of lignin and cellulose (Peay et al. 2008), thereby driving the decomposition of plant materials.

Fungal fruiting morphologies are as diverse as their ecosystem functions and include highly specialised spore dispersal mechanisms. Spores of many fungi are wind dispersed, which allows for long distance dispersal; however, up to 95% of the spores still fall within just a metre of the fruiting body (Galante et al. 2011; Horton et al. 2013). Animals are both active and passive dispersers of fungi. Through consumption, travel and defecation, animals vastly increase the potential range of fungal spore dispersal (Danks 2011; Nuñez et al. 2013; Horton 2017). Some invertebrates are also active dispersers; ambrosia beetles, for example, carry fungi in special pouch-like organs (Hulcr and Stelinski 2017). Many animals get spores caught in their feathers or fur and thus inadvertently become dispersers (Heald and Studhalter 1913; Warner and French 1970; Francesca et al. 2013; Alfonzo et al. 2013). It is possible that the dispersal advantage of mycophagy has driven many fungi to evolve sequestrate fruiting morphologies that are primarily dependent on animals for their dispersal (Fogel and Trappe 1978; Horton 2017; Elliott and Trappe 2018; Koch and Aime 2018). Similar to selective pressures among fungi, environmental factors have produced a diversity of morphologies in birds; these morphological and physiological differences mean that there are many types of feeders, ranging from specialists to generalists. Some raptors spend energy aerially hunting for food, while large-bodied ground foraging birds spend their energy scratching and seldom fly. There are energetic pros and cons for these and a multitude of other foraging methods that have arisen in different bird lineages. Some groups of birds, such as hummingbirds, pelagic birds and vultures, have specialised modes of foraging or specialised habitats that are unlikely to lead to mycophagy and the dispersal of fungi through scats. Other groups of birds, such as ground foragers, are far more likely to be regularly eating and therefore dispersing fungi.

Birds come in contact with fungi and fungal spores throughout their environments and disperse fungi in ways other than just mycophagy. Cavity-dwelling and cavity-excavating birds form close associations with fungi that are thought to soften the wood and enable birds' cavity excavation; in turn, the birds may help to disperse the fungi (Jackson and Jackson 2004; Jusino et al. 2016). Birds may also be dispersing spores through nesting and courtship behaviours that involve fungi (McIlveen and Cole 1976; Aubrecht et al. 2013; Elliott and Marshall 2016; see "Bird-fungal associations among bowerbirds and open nest building birds" section).

Regardless of whether or not birds ingest fungal fruiting bodies or move spores by other means, they are playing an important role in the dispersal of fungi. Given the large migratory ranges of some species, birds have the potential to be one of the biggest factors in fungal distribution and dispersal; yet they have attracted little attention in this regard. The primary objectives of this review are to collect and evaluate current knowledge of the ecosystem impacts of symbiotic bird-fungal associations, evaluate and suggest means of addressing existing limitations in bird dietary studies and identify areas requiring further research.

## Methods and limitations

This manuscript highlights key areas of study within bird-fungal associations. The overall goal is to increase understanding of the ecological impacts of potentially beneficial symbiotic associations between birds and fungi, particularly those associations involving diets and nesting. This paper does not review associations between birds and fungal pathogens, and the reviewed associations between birds and non-pathogenic fungi are limited to those that involve nesting and feeding behaviour. Bird associations with fungal pathogens—particularly those involving migratory birds—have played a major role in the dispersal of otherwise regional pathogens (Heald and Studhalter 1913, 1914; Warner and French 1970; Malloch and Blackwell 1992; Hubálek 2004; Thomas et al. 2008). However, we consider fungal pathogens and their associations with birds to be outside the scope of this review. Many associations between birds and non-pathogenic fungi fall outside of the nesting and feeding realm but are ubiquitous in ecosystems around the world. Though outside the scope of this review, there are numerous reports of microscopic fungi forming non-pathogenic associations with birds (Pugh 1964; Warner and French 1970; Farris et al. 2004; Cafarchia et al. 2006; Alfonzo et al. 2013; Francesca et al. 2013; Belisle et al. 2014; da Silva et al. 2016; Theron-De Bruin et al. 2018; Correia et al. 2019). For researchers interested in either of these types of associations, we recommend the aforementioned studies as good starting points.

Within the areas covered, we have sought to make this review as comprehensive as possible. We aim to demonstrate the diversity of bird and fungal species involved in these associations. In the literature reviewed, authors were sometimes unclear about the identity of associated fungi

even at the generic level; in these cases, we have done our best to provide as much taxonomic specificity as possible.

For practical reasons, we have restricted our search of literature to that written in English, German and Spanish; one French and one Italian paper were also included. The majority of the relevant literature has been written in English, though there is a substantial amount of Spanish literature on rhizomorph use in nests. We used a variety of relevant search terms and key words, carefully examined cited reference lists within relevant papers and conducted methodical searches in relevant journals, databases and search engines for papers about the behaviours and diets of hundreds of bird species in relation to fungi and their dispersal. Depending on the known behaviours of some species, genera, families and orders, we put more or less effort into seeking out literature about their associations with fungi. For example, in reviewing dietary studies, limited effort was devoted to reviewing hummingbird diets, while substantial effort was devoted to that of various groups of ground foraging birds; in reviewing rhizomorph usage in nests, limited effort was devoted to reviewing the nesting material of penguins, but substantial effort was concentrated on arboreal nesting birds living in regions where fungal rhizomorphs are common. In the cavity-nesting portions of this review, we focused on birds that are primary excavators in wood instead of ground or cliff nesting species.

A problem in reviewing literature for the dietary section of this review lies in that there is almost no consistency in terms used by researchers referring to fungal consumption. For example, among papers dealing with diets, authors refer to the action or trait of eating fungi as any of the following: mycophagy, mycophagous, fungivory, fungivore, endozoochorous, mushroom eating, or fungus eating (Table 1). Other papers use none of these terms and only mention a fungus in the diet list. Terms describing the food item range from a formal species name to general terms including toadstool, shelf-mushroom, bracket fungus, truffle and puffball. Inconsistent and non-standard terminology hinders the development of a coherent body of knowledge and ultimately the understanding of ornithomycological relationships.

There is generally more detail in the literature concerning the taxonomy of fungi associated with cavity-dwelling species, but some of the early papers only made comments about "rotted" or "soft" wood and did not attempt to identify the fungi forming the associations. The search terms here are also wide-ranging. Among open-nesting birds and bowerbirds, the terms used for fungi also varied substantially; sometimes the fungi were not initially recognised as fungi until further study of the nests was conducted.

We hope this paper serves as a foundation for further research on and understanding of these ecologically important bird–fungal associations.

## Bird mycophagy and spore dispersal

Simpson (1998, 2000) has published the only known papers evaluating bird mycophagy. These listed 27 species to be mycophagous; but since they were published in two regional mycological journals with relatively narrow readership, the papers have not been widely read or cited. Aside from these two papers, we only found scattered reports of mycophagy; these were usually in the observational notes section of journals or buried in dietary lists (Table 1).

Mycophagy has been far more thoroughly studied among mammals, with more than 300 published papers reporting more than 260 mammal species on six continents to eat fungi; some mammal species are the subject of more than a dozen papers reporting on these associations (Fogel and Trappe 1978; Claridge and May 1994; Bozinovic and Muñoz-Pedreros 1995; Elliott et al. 2019; Elliott unpublished data). Many mammal species and genera are known to depend on fungi for the majority of their diets (Maser et al. 2008); but among birds, only pygmy parrots (*Micropsitta* spp.) are currently suspected to rely heavily on fungi and lichens for food (Rand 1942; Forshaw 1989). Birds arguably occupy an equal if not greater diversity of niches than mammals, and there are nearly twice as many described species of birds (Gill and Donsker 2018) as there are mammals (Wilson and Reeder 2005).

The question remains: Why is there such a large disparity between reports of mycophagy in mammals and in birds? It is possible that low levels of sugars in fungi may make them less appealing to birds (Simpson 1998). This hypothesis may be relevant for birds with very specialised diets (e.g. hummingbirds and honeyeaters); but many birds have diverse omnivorous diets (Lopes et al. 2016), and fungi are high in amino acids, protein and water (Vogt et al. 1981; Cork and Kenagy 1989; Hussain and Al-Ruqaie 1999; Claridge and Trappe 2005; Kalač 2009; Wallis et al. 2012). Given the nutritional value of fungi and the fact that their cells are composed of chitin (the same as invertebrate cells frequently eaten by birds; Cork and Kenagy 1989), there is evidence against the lack of nutrient value hypothesis. There has also been substantial research showing benefits in feeding fungi to farmed poultry (Bederska-Łojewska et al. 2017). In feeding studies of broiler chickens, various Basidiomycota were added to feeds; depending on fungal species used, broilers generally showed increased body weight gain and improved resistance to pathogens (Bederska-Łojewska et al. 2017). Many

**Table 1** Bird mycophagy

| Bird family | Common and Latin names | Citations | Fungi in diet[a] | Methods used[b] |
|---|---|---|---|---|
| Acanthizidae | Pilotbird (*Pycnoptilus floccosus*) | Zwart (1973) | Small mushrooms | Observation |
| Alaudidae | Hoopoe Lark (*Alaemon alaudipes alaudipes*) | Alsheikh and Trappe (1983b) | *Phaeangium lefebvrei* | Observation |
| | Bifasciated Lark (*Alaemon alaudipes doriae*) | Alsheikh and Trappe (1983b) | *Phaeangium lefebvrei* | Observation |
| | Bar-tailed Lark (*Ammomanes cinctura*) | Alsheikh and Trappe (1983b) | *Phaeangium lefebvrei* | Observation |
| | Desert Lark (*Ammomanes deserti*) | Alsheikh and Trappe 1983b | *Phaeangium lefebvrei* | observation |
| | Temminck's Horned Lark (*Eremophila bilopha*) | Alsheikh and Trappe (1983b) | *Phaeangium lefebvrei* | Observation |
| | Horned Lark (*Eremophila alpestris*) | Alsheikh and Trappe (1983b) | *Phaeangium lefebvrei* | Observation |
| | Crested Lark (*Galerida cristata*) | Alsheikh and Trappe (1983b) | *Phaeangium lefebvrei* | Observation |
| | Theckla's Lark (*Galerida thecklae*) | Alsheikh and Trappe (1983b) | *Phaeangium lefebvrei* | Observation |
| Cacatuidae | Yellow-tailed Black Cockatoo (*Calyptorhynchus funereus*) | Taylor and Mooney (1990) | Hyphomycetes and slime mould (possibly a resupinate crust) | Observation |
| Casuariidae | Emu (*Dromaius novaehollandiae*) | Simpson (1998) | *Lycoperdon* and *Bovista* | Observation |
| | Southern Cassowary (*Casuarius casuarius*) | Crome (1976) | Bracket fungi | GI sample |
| Climacteridae | Brown Treecreepers (*Climacteris picumnus*) | Doerr and Doerr (2002) | Filamentous fungus and Agaricaceae | Observation |
| | White-throated Treecreeper (*Cormobates leucophaea*) | Maurer et al. (2017) | *Laetiporus portentosus* | Observation |
| Columbidae | Bronze Ground Dove (*Alopecoenas beccarii intermedius*) | Weeks et al. (2017) | Fungus | GI sample |
| | Kererū (*Hemiphaga novaeseelandiae*) | Rawlings (1956), McEwan (1978), Clout et al. (1986), and O'Donnell and Dilks (1994) | *Cyttaria* spp. | Observation |
| Corvidae | American Crow (*Corvus brachyrhynchos*) | Webster (1902) | *Agaricus campestris* | Observation |
| | Gray Jay (*Perisoreus canadensis*) | Bailey (1904), Sutherland and Crawford 1979, and Alsheikh and Trappe (1983b) | Toadstools; myxomycete plasmodium; *Pleurocybella porrigens* and *Rhizopogon* sp. | Observation |
| | Siberian Jay (*Perisoreus infaustus*) | Andreev (1978) | Fungi | GI sample |
| Cracidae | Yellow-knobbed Curassow (*Crax daubentoni*) | Bertsch and Barreto (2008) | Dyscomicetes/fungi | GI sample |
| Dinornithidae | South Island Giant Moa (*Dinornis robustus*) | Boast et al. (2018) | *Armillaria*, *Cortinarius* or *Inocybe* | Genetics |
| Furnariidae | Lark-like Brushrunner (*Coryphistera alaudina*) | Olrog (1955) | Hongos (mushroom) | Observation |
| Glareolidae | Cream-colored Courser (*Cursorius cursor*) | Alsheikh and Trappe (1983b) | *Phaeangium lefebvrei* | Observation |
| Megalapterygidae | Upland Moa (*Megalapteryx didiformis*) | Boast et al. (2018) | *Armillaria*, *Cortinarius* or *Inocybe* | Genetics |
| Megapodiidae | Australian Brushturkey (*Alectura lathami*) | Simpson (1998, 2000) | *Mycena* sp.; *Lentinula lateritia* | Observation |
| | Malleefowl (*Leipoa ocellata*) | Benshemesh 1992 and Reichelt and May (1997) | Mostly *Mycena* spp. and *Laccocephalum mylittae*; *Paxillus* sp. | Observation |
| Meliphagidae | White-plumed Honeyeater (*Ptilotula penicillata*) | McKeown (1934) | Fungi | GI sample |

**Table 1** (continued)

| Bird family | Common and Latin names | Citations | Fungi in diet[a] | Methods used[b] |
|---|---|---|---|---|
| Menuridae | Superb Lyrebird (*Menura novaehollandiae*) | Elliott and Vernes (2019) | *Agaricus* sp., *Descolea* spp., *Hypholoma* sp., *Hysterangium* spp. *Rossbeevera vittatispora*, Russulaceae, *Scleroderma* sp. and several unidentified taxa | Micro-analysis |
| Muscicapidae | European robin (*Erithacus* cf. *rubecula*) | Hastings and Mottram (1914) | *Agaricus campestris* | Observation |
| Odontophoridae | California Quail (*Callipepla californica*) | Alsheikh and Trappe (1983b) | *Suillus* spp. | Observation |
| | Northern Bobwhite (*Colinus virginianus*) | Laessle and Frye (1956) and Miller and Halls (1969) | *Rhizopogon* sp.; mushrooms | ?; GI sample |
| Petroicidae | Eastern Yellow Robin (*Eopsaltria australis*) | Simpson (2000) | *Gymnomyces* sp. (sequestrate *Russula*) | Observation |
| | North Island Robin (*Petroica longipes*) | Medway (2000) | *Armillaria limonea* | Observation |
| Phasianidae | Ruffed Grouse (*Bonasa umbellus*) | Gross (1937), Kittams (1943), Brown (1946), Stewart (1956), Miller and Halls (1969), McGowan (1973), Rose and Parker (1983), and Tanney and Hutchison (2011) | Fungus and mushroom; fungi; gilled fungi; Agaricaceae; mushrooms; Basidiomycetes; mushrooms; *Lactarius*, *Melanoleuca*, *Russula* spp. | GI sample; observation |
| | Wild Turkey (*Meleagris gallopavo*) | Miller and Halls (1969) and Trappe unpublished data | Mushrooms; *Tuber* sp. | ?; micro-analysis |
| | Willow Ptarmigan (*Lagopus lagopus*) | Williams et al. (1980) | Fungi | GI sample |
| | Spruce Grouse (*Falcipennis canadensis*) | Crichton (1963), Ellison (1966), Stoneberg (1967), Pendergast and Boag (1970), and Franceschi and Boag (1991) | Basidiomycete; Basidiomycete; Basidiomycete; fungi; 31 taxa of fungi (*Russula* is the only name mentioned) | GI sample; observation |
| | Ring-necked Pheasant (*Phasianus colchicus*) | Dutton and Bolen (2000) | Mushroom | GI sample |
| | Chicken (*Gallus gallus domesticus*) | Elliott and Vernes (2019) | *Armillaria gallica*, *Entoloma abortivum* and *Hypholoma sublateritium* | Observation |
| Prunellidae | Black-throated Accentor (*Prunella atrogularis*) | Alsheikh and Trappe (1983b) | *Phaeangium lefebvrei* | Observation |
| Psittacidae | Austral Parakeet (*Enicognathus ferrugineus*) | Diaz and Kitzberger (2006) and Díaz et al. (2012) | *Cyttaria*; *Cyttaria* | Observation |

**Table 1** (continued)

| Bird family | Common and Latin names | Citations | Fungi in diet[a] | Methods used[b] |
|---|---|---|---|---|
| Psittaculidae | Australian King-Parrot (*Alisterus scapularis*) | Elliott and Elliott (2019) | *Cyttaria septentrionalis* | Observation |
| | Buff-faced Pygmy-parrot (*Micropsitta pusio*) | Bell (1984); Forshaw (1989), and Sam et al. (2017) | Fungi (taxonomically ambiguous) | Observation |
| | Finsch's Pygmy Parrot (*Micropsitta finschii*) | Bradley and Wolff 1956, Schodde 1977, and Forshaw (1989) | Fungi (taxonomically ambiguous) | GI sample; observation |
| | Meek's pygmy parrot (*Micropsitta meeki*) | Sibley (1951) | Fungi (taxonomically ambiguous) | Observation |
| | Red-breasted Pygmy Parrot (*Micropsitta bruijnii*) | Rand (1942), Greensmith (1975), Schodde (1977), Ivereigh (2001), Sam et al. (2017), and Weeks et al. (2017) | Multiple species taxonomy unclear; jelly fungi and lichen | GI sample; observation |
| | Yellow-capped Pygmy Parrot (*Micropsitta keiensis*) | Forshaw (1989) | Fungi (taxonomically ambiguous) | Observation |
| Strigidae | Southern Boobook (*Ninox novaeseelandiae*) | Ritchie and Martin (2006) | *Pisolithus albus* | Observation |
| Strigopidae | Kakapo (*Strigops habroptilus*) | Forshaw (1989), Powlesland et al. (2006), and Boast et al. (2018) | Fungi (taxonomically ambiguous); *Armillaria*, *Cortinarius* or *Inocybe* | ?; genetics |
| Thraupidae | Yellow-faced Grassquit (*Tiaris olivaceus*) | Ramirez-Fernandez et al. (2019) | Mold | Observation |
| Turdidae | Common Blackbird (*Turdus merula*) | Hastings and Mottram (1914) | *Hypholoma sublateritium* | Observation |
| | Thrush (*Turdus* sp.) | Hastings and Mottram (1914) | *Hypholoma sublateritium* | Observation |
| | Austral Thrush (*Turdus falcklandii*) | Rozzi (2004) | *Cyttaria* spp. | Observation/folklore |
| Upupidae | Eurasian Hoopoe (*Upupa epops*) | Alsheikh and Trappe (1983b) | *Phaeangium lefebvrei* | Observation |

List of 54 species of birds documented to eat fungi. This list relies on the taxonomic abilities of the cited authors. We made every effort to only include reports of macro fungi in this table; however, some authors reporting on the diets of members of the Psittaculidae were at times very ambiguous regarding whether lichens and/or fungi were consumed

[a]Fungal names in this table reflect updated nomenclature (as per IndexFungorum and MycoBank) and are not necessarily the same as what appears in the original texts. Methods used by some of the cited authors may not have been reliable; but since there are no voucher specimens for most of these studies, we were unable to confirm or disprove any identifications

[b]Key to methods: *Genetics* DNA sequences were extracted from scats, and mycophagy was assumed based upon sequence data. *GI sample* Macroscopic examination of part of the gastrointestinal tract (crop, gizzard, stomach, etc.); if macroscopically recognisable fungal remains were found, mycophagy was assumed. *Micro-analysis* Microscopic examination of scats was performed at a minimum of ×400 magnification; if spores were detected at high densities, mycophagy was assumed. *Observation/folklore* Traditional knowledge/stories based on observations of feeding behaviour were used to indicate mycophagy. *Observation* The author of the original publication reported seeing bird(s) feeding on fungi. *?* Indicates that authors of original publications were unclear on how mycophagy was determined

of the studies reviewed by Bederska-Łojewska et al. (2017) showed this to be true even when fungal supplements were at low percentages (as low as 2%). During the First World War, the Austrian agency responsible for animal management also recommended dried mushrooms as a good food source for laying hens (Anon 1916). Furthermore, Andreev (1978) showed that during cold northern Eurasian winters, Siberian Jays (*Perisoreus infaustus*) relied heavily on the nutritional value of fungi in their diet to survive, likely stealing much of what they ate from rodent caches. These studies indicate that at least some birds have the physiological ability to access nutrients from fungi, and even small quantities of fungi can significantly impact bird health.

Mammals frequently feed on underground fungi (truffles) that they detect primarily by smell (Mills 1978; Vernes et al. 2015). Many birds are thought to rely heavily on visual cues in foraging and are thought to have less acute olfactory senses than many mammals, but some bird species such as the Kiwi (*Apteryx* sp.), Yellow-backed Chattering Lories (*Lorius garrulus*) and Kakapo (*Strigops habroptilus*) have been shown to have highly developed senses of smell (Wenzel 1968; Roper 2003; Hagelin 2004). Recent research has indicated that many birds may be able to detect more odours than previously thought (Hagelin and Jones 2007). Birds can likely detect some aromas from fungi, but whether or not fungal odours are significantly relevant to bird mycophagy has not been studied. Regardless of the relevance of fungal aromas, birds are known for their keen eyesight (Cuthill et al. 2000; Ödeen and Håstad 2003; Zueva et al. 2014). Fungi exhibit numerous distinctive shapes, sizes and colours, so it is reasonable to surmise that birds could easily detect fungi by sight.

The paucity of reports of mycophagy by birds can most likely be explained by current sampling methods that do not allow for the detection of fungi in diets. Many groups of mammals we now know to rely heavily on fungi for food were historically thought to not eat any. This belief was due to two key flaws in the methods of early dietary studies, which have been mostly remedied by mammalogists and are beginning to be addressed in similar avian studies. First, it is unrealistic and unreliable to gather a large data set on mycophagy through observational studies of bird feeding behaviour alone. When an animal lowers its head, it is often very difficult to determine whether it is ingesting an invertebrate, a seed, a fungus, or a plant shoot. The second methodological flaw occurs in processing samples from digestive tracts. Fungal spores generally survive animal digestive tracts (Colgan and Claridge 2002), but the most common fungal spores are less than 30 μm in diameter and easily lost through sieves. Many zoologists study diets by sifting crop, stomach and faecal samples through coarse strainers (resulting in the loss of most fungal spores) and/or examining remains at relatively low magnification, thereby overlooking spores entirely. The magnification used to identify plant and animal remains is typically too low (less than ×400) to detect the presence of fungi. Since most fungal tissues are soft, they tend to be masticated beyond the point of macromorphological recognition while still in the animal's mouth, and definitely so by the later end of the digestive tract. Thus, it seems reasonable to assume that most fungal material is overlooked, lost or indistinguishable in current standard approaches to bird diet studies; this may very well have led to preconceptions that fungi are either not present or are of limited importance in bird diets.

Studies of bird crops only occasionally report fungi, and normally only in the rare instance when large pieces remain intact. In studying spruce grouse (*Falcipennis canadensis*) mycophagy, Franceschi and Boag (1991) suggested that: "…soft materials, such as fungal tissues, may tend to bypass the crop and enter the proventriculus directly." They also found that grouse tend to eat fungi in larger quantities early in the day. Studies of bird digestive physiology have shown that among chickens subjected to periods of fasting, peristalsis takes the first meal directly to the gizzard; the opening of the crop remains closed (Ziswiler and Farner 1972). This highlights another possible flaw in the methods used for studying birds with crops; even if fungi are in a bird's diet, they may not always pass through the crop. Previous crop and diet studies have likely overlooked fungi for one or more of these reasons. These problems can be easily resolved through molecular dietary analysis or by making microscope mounts of avian gut lavage or faecal samples and studying them at ×400 magnification or higher.

The role that birds play in fungal dispersal has been largely overlooked. We found reports of 54 bird species in 27 families that eat fungi (Table 1); but despite these numbers, bias is readily apparent. In 59 publications directly reporting mycophagy in non-captive birds, only one published study reported microscopic analysis with magnification high enough to detect fungal spores in the scats of one bird species. Of the other 53 bird species, 37 (68.5%) of these were determined to eat fungi based solely on field observations, seven (13%) were determined by examining gastrointestinal (GI) samples of crop/stomach/scat studied at low magnification, two (4%) were determined by using DNA-based molecular approaches (genetics), one (2%) was unclear in its methods, one (2%) used GI samples and unstated methods, four (7%) used field observations and GI samples and one (2%) used genetics and unstated methods.

In contrast, a preliminary review of modes of assessing mammalian mycophagy that the first author is currently

conducting found that few determinations were based only on field observations and most studies determined mycophagy through microscopic examination of scats (Elliott unpublished data). The exception is camera trapping studies where mycophagy was the specific focus of the research (Vernes et al. 2014; Vernes and Jarman 2014). Rodents—many of which dry and cache fungi in obvious locations— are also exceptions, but most other mammals reported to be regular mycophagists have seldom or never actually been observed eating fungi; however, an appropriate microscopic examination of their scat quickly showed otherwise. This reinforces the need to utilise suitable methods to reliably understand vertebrate mycophagy.

Elliott and Vernes (2019) showed how appropriate methods in a diet study revealed mycophagous behaviour in the otherwise well-studied Superb Lyrebird (*Menura novaehollandiae*). This species is omnivorous, and its foraging behaviour puts it in regular contact with fungi. Mycophagy was not observed when watching the birds forage, but when the scats were examined microscopically, they were found to contain spores of approximately 14 different species of fungi (Elliott and Vernes 2019). Previous papers on the diet of this bird either do not mention fungi or only speculated that mycophagy might occur; none provide evidence of fungal consumption (Simpson 1998, 2000). The shift from observation alone to a focus on improving detection via suitable collection and microscopic study of scats was critical to the success of the Elliott and Vernes (2019) study. Adopting these approaches in avian dietary studies will make it possible to more completely understand diets and nutrition of birds and the role birds play in fungal dispersal.

There has been a recent rise in the implementation of molecular-based approaches in dietary studies. Though DNA is a useful tool, it is risky to base determination of mycophagy solely on molecular methods; additional morphological examination of scats and other appropriate controls help to rule out the possibility of contamination. If the DNA of a fungus or other biological material is detected from a scat, it does not necessarily mean that the organism was eaten. With improved DNA-based methods, true biological replicates, careful sampling and positive and negative controls taken through each step of the process, it is feasible to reliably detect contamination in high-throughput sequencing data; but current sequencing technology does not allow for estimation of copy number, let alone spore numbers (Nilsson et al. 2018; Palmer et al. 2018; Jusino et al. 2019). Regardless of the methods used, without the appropriate use of controls, it is still very difficult to determine whether fungal DNA presence indicates consumption. DNA-based analysis also detects non-reproductive material, making it problematic to determine if fungi detected through sequencing are actually being dispersed by animals. Ultimately, the most rigorous and informative approach is to pair sequence data with microscopic examination. The molecular data can help to clarify the taxonomy of spores detected using a microscope, and the microscopic methods can help to clarify whether or not reproductive tissues of the molecularly-detected fungi are actually present.

Some studies have used stable isotope tracking to detect fungi in the diets of wildlife and prehistoric humans (McIlwee and Johnson 1998; O'Regan et al. 2016). It is technologically possible to use carbon-isotopes to differentiate fungi from other dietary components; to our knowledge, these methods have never been applied in the search for fungi in bird diets. Isotope tracking is another plausible method that could be used to study bird mycophagy, but it would likely provide similar data to what can be generated through other methods.

The bird species listed in Table 1 are examples of primary mycophagists, but birds can also be secondary dispersers of fungi. Many species, ranging from shore birds to turkeys, eat a wide array of insects that eat fungi (Dalke et al. 1942; Morrison and Hobson 2004; Wilding et al. 2012; Watson and Shaw 2018). These insects are well-documented to contribute to fungal dispersal, but if they are eaten by a migratory bird that flies between islands or even between continents, the dispersal potential of the fungal spores could be dramatically increased. The veiled polypore *Cryptoporus volvatus* forms close associations with insects that reside in its fruiting bodies and serve as spore dispersers (Kadowaki 2010); woodpeckers have been observed tearing open the fruiting bodies of this mushroom and eating its associated insects (Watson and Shaw 2018). This would inevitably lead to the woodpeckers serving as secondary dispersers of the spores of *C. volvatus*. Some raptors such as the Southern boobook (*Ninox novaeseelandiae*) have been reported to directly feed on fungi (Ritchie and Martin 2006), but they are potentially also secondary dispersers of fungi. Raptors eat smaller birds and small mammals, many of which have been shown to eat large quantities of fungi (Pearson and Pearson 1947; Maser et al. 1985; Ovaska and Herman 1986; Trappe 1988; Vernes et al. 2004, 2015; Nuske et al. 2017). After catching a mammal, many raptor species gut their prey, leaving behind a gastrointestinal tract (Forsman et al. 2004). Cough pellets (regurgitated, undigested parts of food) left by raptors are another likely mode of secondary dispersal. We have found one study that demonstrated that there can be many fungi present in cough pellets of the common kestrel (*Falco tinnunculus*) (Watling 1963). However, the methods applied by Watling would have been unlikely to detect the presence of fungi ingested by the kestrel's prey animals; so this study sheds little light on secondary dispersal of fungi by raptors. Regardless of whether or not spores end up on

their wings or in cough pellets, scats or discarded gastrointestinal tracts, raptors are almost certainly dispersing spores.

## Examples of implications of bird mycophagy

There are major gaps in knowledge of bird mycophagy. But despite the lack of information currently in the literature, we show that at least 54 bird species in many regions of the world eat fungi (Table 1). We speculate that, as with mammal-fungal interactions, bird mycophagy contributes to a diversity of ecosystem functions. Many fungal species consumed by birds are mycorrhizal; i.e., they play a vital role in the uptake of nutrients by plants. These fungi have many modes of spore dispersal, but vertebrates rank among the most effective vectors (Fogel and Trappe 1978; Maser et al. 2008; Danks 2011; Galante et al. 2011; Nuñez et al. 2013; Wood et al. 2015). Many species of myxomycetes, which are in Kingdom Protista but in some ways function similarly to fungi, have unusually cosmopolitan distributions; this has sparked debate about their mode of dispersal. Birds may be contributing to these widespread distributions by consuming myxomycetes or substrates that contain them (Sutherland and Crawford 1979; Suthers 1985).

Birds contribute to regional fungal spore dispersal and may play a role in the long distance or even transcontinental distribution of some groups (Orihara et al. 2016; Elliott and Vernes 2019; Hobart 2019). As has been shown with some rodents, it is possible that corvids deposit scats laden with fungal inoculant in the same habitats where they cache seeds and nuts (Pirozynski and Malloch 1988; Beever and Lebel 2014). Given what is known about the durability of fungal spores and that they remain viable after passage through the guts of mammals (Trappe and Maser 1976; Kotter and Farentinos 1984; Lamont et al. 1985; Claridge et al. 1992; Sarasini and Pina 1995; Colgan and Claridge 2002; Caldwell et al. 2005; Piattoni et al. 2014; Correia et al. 2019), we suspect similar results are true for birds; however, further testing is needed.

There are currently no groups of fungi that are thought to depend entirely on bird dispersal, but there are some hypotheses suggesting that the spore packets (peridioles) produced by members of the Nidulariaceae (sometimes called bird nest fungi) may have evolved associations with seed foraging birds who mistakenly eat them (Sarasini and Pina 1995; Reichholf and Lohmeyer 2012). It has also been shown that peridioles of at least some Nidulariaceae species are discharged by rain (Martin 1927). Sarasini and Pina (1995) fed *Crucibulum laeve* peridioles to a canary (*Serinus canaria*) to test the bird consumption and dispersal hypothesis and found that canaries only ate them if the peridioles were mixed with other food; they did, however, find apparently undamaged spores in the scats. This study is inconclusive but the only one of its kind that we are aware of.

In addition to fungal dispersal, foraging disturbances caused by mycophagous mammals provide vital ecosystem functions for water penetration, soil aeration, reduction of fire fuel loads and the improvement of overall soil health (Garkaklis et al. 1998, 2000, 2003, 2004; Valentine et al. 2013; Fleming et al. 2014). Similar but less thoroughly studied disturbances are caused by some of the larger bodied, ground foraging mycophagous birds (Watling 1985; Nugent et al. 2014; Elliott and Vernes 2019). Additionally, the habits of larger mycophagous vertebrates create disturbances that provide opportunities for smaller birds and mammals to secondarily forage for fungi that were missed by the larger animals (Trappe in Maser et al. 2008; Elliott and Vernes 2019). These findings suggest that mycophagous birds are performing a range of key ecosystem functions that impact an array of associated organisms, yet many of these interactions have not yet been described.

Mycophagous interactions are ubiquitous throughout the world. For example, the arid portions of North Africa and the Middle East are home to a diversity of truffles that form mycorrhizal associations with the shrub genera *Cistus* and *Helianthemum*, both in the family Cistaceae (Alsheikh and Trappe 1983b; Bokhary 1987; Alsheikh 1994; Mandeel and Al-Laith 2007; Bradai et al. 2015). These shrubs depend on their desert truffle symbionts to uptake nutrients, and the truffles likely depend in part on birds for their spore dispersal (Alsheikh 1994). The symbiosis between these desert shrubs and truffles is vital to overall ecosystem health. The sequestrate and often hypogeous (below ground) fruiting habits of these fungi make them adapted to arid environments. The disadvantage of this fruiting morphology is that for their spores to be dispersed, hypogeous fungi must either be eaten by an animal or dry up and have the wind blow the surrounding sand and spores away (Alsheikh and Trappe 1983a, b; Alsheikh 1994). The diversity of animals that eat and disperse fungi in this region is not fully known. Nomadic humans have been eating many of these species since Judeo-Christian biblical times or possibly even earlier (Shavit 2008); though these truffles were typically prepared by cooking, a few groups have been reported to eat them raw (Alsheikh 1994; Bradai et al. 2015; Akyüz et al. 2017). It is possible that some nomadic humans or possibly prehistoric humans served a similar niche as other mycophagous mammals in dispersing symbiotic fungi. This is speculative, as very little is known about prehistoric fungi consumption. But with the loss of nomadic human lifestyles, reduced raw truffle consumption and implementation of waste management systems, desert regions may be facing the loss of humans as

wide-ranging mycorrhizal dispersers. Regardless of what role humans played in this system historically, birds may have filled (and may continue to fill) an equal if not greater role in the dispersal of ecologically significant desert truffles.

Alsheikh and Trappe (1983b) showed that birds may be vital in the dispersal of these mycorrhizal fungi. At least 12 species in this region feed on truffles, and many of these birds migrate widely (Alsheikh and Trappe 1983b; Mandeel and Al-Laith 2007). The use of these fungi by birds has rarely been reported in the literature, but one of the regional names for some desert truffle species roughly translates to mean "bird's fungus", indicating that local people have been and still are aware of an association between fungi and birds (Alsheikh and Trappe 1983b; Mandeel and Al-Laith 2007; Bawadekji et al. 2016). In Bahrain and Turkey, locals look for where birds are gathering to determine where and when the truffles will be fruiting (Mandeel and Al-Laith 2007; Akyüz et al. 2017); in Bahrain, truffles are also used to trap and catch birds (Mandeel and Al-Laith 2007). In some parts of Israel, traps for the sand partridge (*Ammoperdix heyi*) are baited with the truffle *Picoa lefebvrei* (Elinoar Shavit personal communication). Since truffles are used as traditional trap bait, it is likely that the sand partridges and other birds seek out and eat truffles as food; however, we have been unable to find evidence of this in the literature. Bombing and mining have plagued portions of the Middle East since World War II and have ravaged much of the native range of these truffles, thus impacting the entire ecosystem (Alsheikh 1994; Morte et al. 2009). These events presumably have major impacts on birds and other wildlife that feed on truffles and have rippling effects on the regeneration and health of desert plant communities (Omar et al. 2000). Chemicals released into the soil through mining and bombing impact fungi and move through food chains; toxins can be present in the meat and milk of vertebrates that have fed on wild mycorrhizal fungi exposed to chemicals (Hove et al. 1990; Karlén et al. 1991; Avila et al. 1999; Hohmann and Huckschlag 2005). Ultimately, truffle habitat loss and a reduction in truffle productivity are ecological casualties of war and mining in the Middle East; many truffles in that region have been exposed to chemicals that can negatively impact plants, mammals, birds and the ecosystem as a whole. Rose and Parker (1983) investigated metal levels in a population of ruffed grouse (*Bonasa umbellus*) near a copper and nickel smelting operation in Canada and compared these to metal levels in a population 60 km away from the smelting facility. They found that the scats, meat and organs of individuals living close to the smelters had up to 50 times higher nickel and iron levels than those living 60 km away. Fungi were found in the diets of both grouse populations, and the fungi fruiting in each location mirrored the differences in metal contamination. As fungi are known to be bioaccumulators, the fungi in the grouse diets were likely the source of their increased metal levels (Rose and Parker 1983). It is possible that mycophagous bird populations in some Middle Eastern deserts are being similarly impacted by toxins left over from bombing and mining operations.

In June of 2016, the first and third authors visited with Pitjantjatjara elder Rynee Kulitja from the Mutitjulu Community (Northern Territory, Australia). When asked about how she located the edible desert truffle *Elderia arenivaga*, Kulitja indicated that bird calls and behaviour helped to tell her where they were fruiting. We do not know which bird species she was referring to or if this meant that the birds were forming an association with the fungi or even if birds ate this fungus, but it is possible that some of the Australian desert truffles may have similar associations with birds as they do in the Middle East. Further study is needed to fully understand the possible associations between birds and desert truffles.

New Zealand is another region where ecosystem health is likely directly impacted by associations between birds and fungi. Both the North and South Islands are home to a diversity of fungi and birds, but aside from three species of bats, no native terrestrial mammals were present in New Zealand before human arrival; thus, birds may have played (and may still play) a key role in fungal dispersal. Many of New Zealand's sequestrate fungi are unusually brightly coloured (Fig. 1), and their evolution has served as a source of much speculation for mycophagy researchers (Beever 1999; Bougher and Lebel 2001; Lebel 2002; Læssøe and Hansen 2007; Johnston 2010; Beever and

**Fig. 1** A representative selection of two phyla and three genera of the unusually colourful truffles found in New Zealand. The red fruiting bodies without stalks are *Paurocotylis pila* (Pyronemataceae), the purple fruiting bodies are one of the sequestrate species of *Cortinarius* sp. (Cortinariaceae), and the red fruiting bodies with pale-coloured stalks are *Leratiomyces erythrocephalus* (Strophariaceae). These taxa demonstrate some of the colourful fruiting morphologies that may have evolved due to associations with New Zealand birds

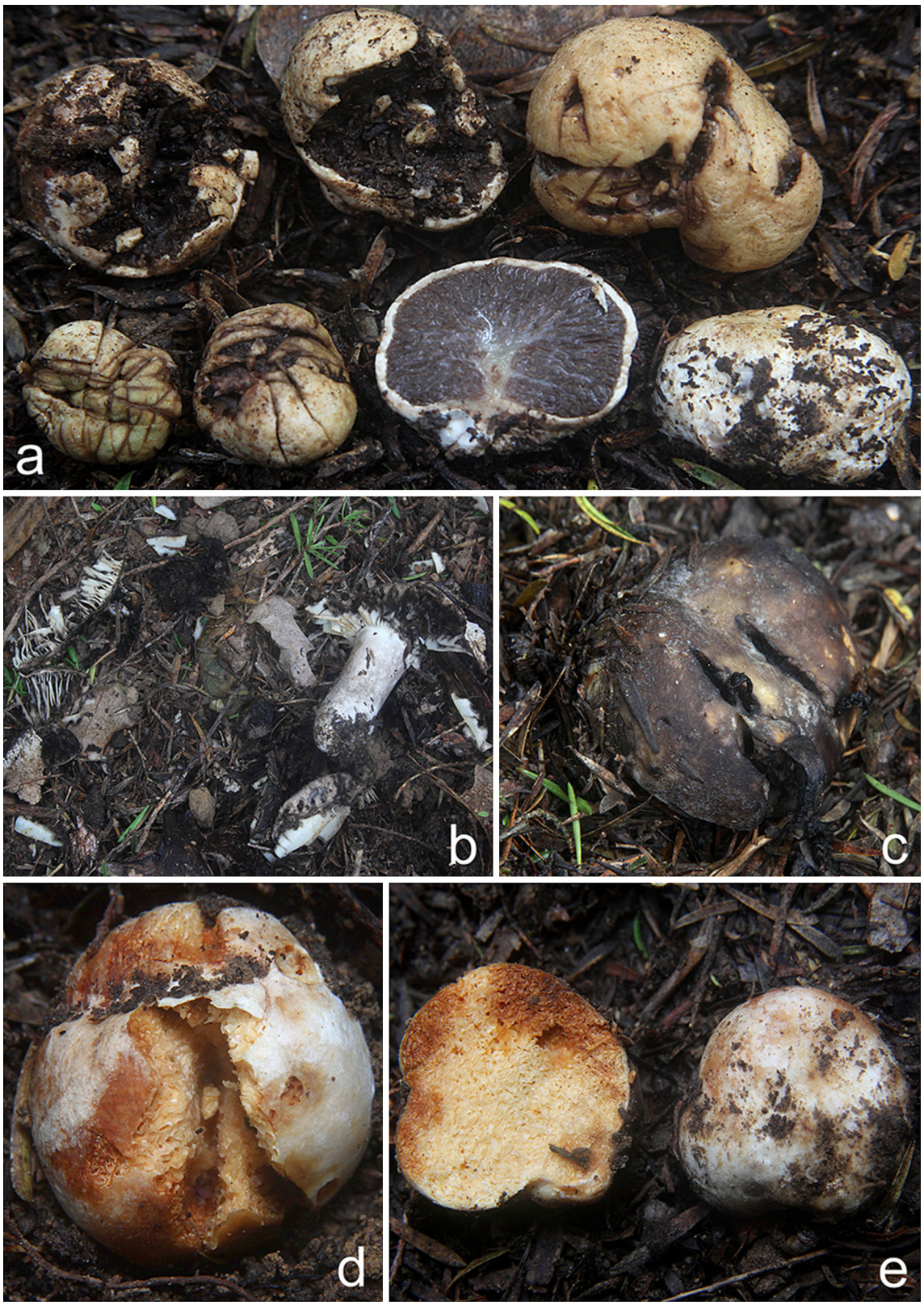
Lebel 2014; Hobart 2019). The bright colours and frequently epigeous (above ground) fruiting habits of these truffle-like fungi may be adaptations by the fungi for ease of detection by visually-cued endemic birds (Beever and Lebel 2014). Some of the fungi eaten by New Zealand birds may mimic the brightly coloured arils or fruits of podocarps (*Podocarpus* spp.), supplejack (*Ripogonum scandens*), passionfruit (*Passiflora* spp.) and *Beilschmiedia* spp. (Beever and Lebel 2014). These associations are plausible but have not been confirmed by observations, experimental work or dietary analysis. Much of New Zealand's landscape has been highly modified, and some endemic birds have either gone extinct or been extirpated from most of their native habitats and are now found only on isolated islands (Miskelly et al. 2008). We thus may never fully understand the interactions that may have occurred between New Zealand birds and truffles. Reduced distributions and otherwise modified assemblages mean that even if valid methods are applied to study modern faecal samples from New Zealand's rare ground foraging birds, we cannot be sure of detecting historic relationships; the surviving birds and their previously associated fungi may no longer be sympatric. Careful molecular and microscopic examination of the stomach and gut contents of pickled museum specimens may help to shed light on some of these relationships.

During April 2017 field studies in Hinewai Reserve near Akaroa, New Zealand, the first author attempted to examine the potential for mycophagy by bird taxa present in the reserve. Study was limited by only being permitted to observe birds rather than conduct mist netting to collect faecal samples. The first author found sequestrate and non-sequestrate fungi representing at least three genera (*Amanita*, *Hysterangium*, and *Russula*) that had been partially eaten by birds (Fig. 2), though he was unable to determine which bird species were actually responsible for consuming the fungi. There were a diversity of birds feeding on the forest floor in this area, and there was considerable variation in the size and nature of peck marks found on the fungal fruiting bodies (Fig. 2). Multiple species were likely responsible for the consumption of fungi in this system.

A detailed study of faecal samples of New Zealand birds is needed to further our understanding of mycophagy in the region. In their 2018 study, Boast et al. used molecular tools to study the coprolites of extinct New Zealand Moas; they suggest that some species of these extinct birds may have eaten fungi. Though fungi have almost certainly been identified in these coprolites, Boast et al. obtained their sequences by using general eukaryotic 18S primers (Euk1391f and EukBr) that amplify a ~ 210 to 310 bp fragment (http://www.earthmicrobiome.org/protocols-and-standards/18s/). It is possible that if these DNA were to be amplified with more specific primers—perhaps from the internal transcribed spacer region (ITS), as well as additional loci (i.e. 28S)—even better resolution of fungal groups represented in the samples could be obtained. If these samples were to be examined under a microscope, the presence of spores would allow for even more detailed understanding of the taxonomy of fungi involved.

Another bird-fungal association specific to the Southern Hemisphere involves the ascomycete genus *Cyttaria*. This fungus produces fruiting bodies that often grow in large clusters on southern beech (*Nothofagus* sensu lato) species in Australia, New Zealand and southern South America; the fungus is absent, however, from the beech forests of New Guinea and New Caledonia (Korf 1983). The kererū (*Hemiphaga novaeseelandiae*), austral parakeet (*Enicognathus ferrugineus*) and Australian king-parrot (*Alisterus scapularis*) have been observed eating *Cyttaria* fruitings (Rawlings 1956; McEwan 1978; Clout et al. 1986; O'Donnell and Dilks 1994; Diaz and Kitzberger 2006; Díaz et al. 2012; Elliott and Elliott 2019). In an anthropological study of bird lore among the Yahgan peoples of far southern South America, Rozzi (2004) recorded a story involving an austral thrush (*Turdus falcklandii*) eating *Cyttaria* spp. It is possible that this fungus has evolved a mistletoe-like association with birds and arboreal mammals that may help with its dispersal through the forest canopy (Elliott and Elliott 2019).

This manuscript shows that bird mycophagy occurs in disparate ecosystems; and though it likely occurs much more frequently and widely than what is shown in the literature, the prevalence of mycophagy has historically been overlooked and/or unaccounted for in study methods. Further exploration of this phenomenon is needed to evaluate the presence of avian mycophagy and what role it plays in the ecosystems of the regions discussed and others around the world. Mycophagous interactions are important to the conservation of organisms involved and to the ecosystem as a whole. It has become increasingly difficult for some mycophagous mammals to maintain healthy populations in human-engineered landscapes, and this has led to a decrease in dispersal of the key ectomycorrhizal fungi on which many woody plants depend (Johnson 1996; Nguyen et al. 2005; Vernes 2010; Dundas et al. 2018). Given that many birds move between fragmented forests, they may represent a key means of moving fungi between anthropogenically separated systems. These links will likely prove particularly important in the increasing number of disturbed ecosystems around the world.



◀**Fig. 2** A selection of fungi associated with *Nothofagus* spp. and *Leptospermum* spp. that showed signs of New Zealand bird mycophagy in Hinewai Reserve. **a** A collection of *Hysterangium* (Hysterangiaceae) that had been heavily pecked by birds. Note the clear beak marks on the fruiting body in the upper right corner of the image. There were no signs of insects present in these fruiting bodies. **b** Specimen of *Russula* cf. *inquinata* (Russulaceae) that has been upturned and partially eaten by birds. **c** Upper cap surface of *R. inquinata* showing distinctive bird beak marks. **d** In situ sequestrate *Russula* sp. showing evidence of mycophagy. A bird foraging in the leaf litter had apparently exposed this truffle and consumed part of the fruiting body. **e** Cross section showing the interior of the sequestrate *Russula* sp. that had been partially eaten by a bird

## Bird–fungi interactions among cavity-dwelling birds

Most living wood contains antifungal compounds that prevent fungal decay (Wagener and Davidson 1954; Rayner and Boddy 1988), but the heartwood of trees is physiologically "dead" and does not produce these same chemical defenses found in the sapwood and phloem. If the outer bark (which serves as a protective barrier) is breached by an injury, saprotrophic fungi may enter through the wound and begin to decompose the sapwood and heartwood (Wagener and Davidson 1954; Rayner and Boddy 1988). Using specialised enzymes, these fungi typically break down the lignin and cellulose in the wood and cause it to become soft (Wagener and Davidson 1954; Rayner and Boddy 1988; Monrroy et al. 2011). Decomposition can be constrained by the living tree to small areas, and the trees can live for decades or longer after being infected with decay fungi and serve as important habitat for a variety of animals. It is advantageous for cavity-dwelling animals to have sturdy live wood as the exterior of their cavities instead of excavating hollows in highly decomposed dead trees; strong exterior wood helps to prevent large predators like bears or raccoons from gaining access into cavities and reduces the chance of trunk breakage in periods of high winds (Kilham 1968; Tozer et al. 2009).

Cavity-excavating birds like woodpeckers excavate cavities in trees. This is energetically expensive, especially in the case of relatively hard trees. Thus, woodpeckers are thought to select excavation sites in wood that has been softened by decay fungi (Lawrence 1967; Skutch 1969; Jackman 1974; Conner et al. 1976; Jackson 1977; Harestad and Keisker 1989; Parks and Bull 1996; Jackson and Jackson 2004; Zahner et al. 2012; Jusino et al. 2015; Lorenz et al. 2015). It has been hypothesized that woodpeckers save energy by selectively excavating cavities in trees that are infected with wood-softening fungi; this is termed the "tree selection hypothesis" (Jusino et al. 2015). Cavity-excavating birds may also facilitate the transmission of decay fungi while excavating and subsequently benefit from the decay they bring in. This is termed the "bird facilitation hypothesis" (Jusino et al. 2015). Jusino et al. (2016) found support for the bird facilitation hypothesis through a 26-month field experiment that utilised sterilely drilled excavations that were made to be both accessible and inaccessible to red-cockaded woodpeckers (*Picoides borealis*). Endangered red-cockaded woodpeckers are endemic to the longleaf pine forests of the Southeastern United States and are the most thoroughly studied cavity-excavators in regard to their associations with fungi (Table 2). These woodpeckers have a lengthy excavation process that can range from less than one year to decades (Harding and Walters 2004); historically, they were thought to select trees for excavation based on the presence of one fungus, *Porodaedalea pini*. However, recent DNA-based molecular work has demonstrated that more than 50 putative wood decay taxa are found on the birds and in their excavations, suggesting that red-cockaded woodpeckers are associated with a diverse community of fungi and not just a single taxon (Jusino et al. 2016).

It is difficult to eliminate all other factors and experimentally test the tree selection hypothesis. In support of this hypothesis, observational studies investigating these associations have reported that woodpeckers tend to excavate trees with some evidence of decay (Table 2). The techniques used to determine the presence, prevalence and species of wood-decaying fungi with which cavity-excavating species associate vary, and each has both strengths and weaknesses. Surveys of fruiting bodies on the exterior of excavated trees are widely used, but this method can only detect species that are fruiting at the time of the survey; these typically comprise a small fraction of the total fungal community present in the wood (Rayner and Boddy 1988; Lindner et al. 2011; Jusino et al. 2014). Many trees are visibly healthy and lack fungal fruiting bodies but still harbour decay fungi and softer wood; these have likely led to reports of cavity-excavating birds sometimes excavating cavities in non-decayed trees. Another method is to cut through the wood and visually assess the status/presence of rot. A major limitation to this method is that it is destructive to cavity habitat and consequently may not be used for protected areas or species. A less destructive and more informative assessment technique is culturing and/or DNA-based molecular fungal community characterisation; this technique can identify the presence and taxa of wood-degrading fungi but cannot determine the structural integrity of the wood. It is also feasible to detect the decay status of heartwood by measuring the torque needed to penetrate the wood with a drill (Matsuoka 2000); this technique does little damage to the cavity tree. Sawdust and wood chips can be aseptically collected for culturing or DNA-based molecular work during drilling/boring for decay and wood hardness assessment, provided that these instruments are

**Table 2** Associations between cavity-excavating birds and saprotrophic fungi growing in cavity trees

| Bird family | Bird species | Fungi[a] | Citations |
|---|---|---|---|
| Picidae | Ivory-billed Woodpecker (*Campephilus principalis*) | Unidentified fungi | Allen and Kellogg (1937) |
| | Robust Woodpecker (*Campephilus robustus*) | Unidentified fungi | Cockle et al. (2012) |
| | Northern Flicker (*Colaptes auratus*) | *Cerrena unicolor*; *Fomes* sp.; *Fomes fomentarius*; *Phellinus rimosus*; *Poria* sp.; *Porodaedalea pini*; *Sarcodontia pachyodon*; unidentified fungi | Dennis (1969), Skutch (1969), Conner et al. (1976), McClelland et al. (1979), Miller et al. (1979), Raphael and White (1984), Keisker (1986), Harestad and Keisker (1989), Dobkin et al. (1995), Saab and Dudley (1998), Steeger and Dulisse (2002), Aitken and Martin (2004), Martin et al. (2004), Blanc and Martin (2012), Edworthy et al. (2012), and Lorenz et al. (2015) |
| | Campo Flicker (*Colaptes campestris*) | Unidentified fungi | Cockle et al. (2012) |
| | Green-barred Woodpecker (*Colaptes melanochloros*) | *Fomes fasciatus*; unidentified fungi | Cockle et al. (2012) |
| | White-backed Woodpecker (*Dendrocopos leucotos*) | Unidentified fungi | Hågvar et al. (1990) and Pakkala et al. (2018) |
| | Great Spotted Woodpecker (*Dendrocopos major*) | Unidentified fungi | Hågvar et al. (1990), Glue and Boswell (1994), and Matsuoka (2008) |
| | Lesser Spotted Woodpecker (*Dryobates minor*) | Unidentified fungi | Hågvar et al. (1990), Glue and Boswell (1994), and Pakkala et al. (2018) |
| | Lineated Woodpecker (*Dryocopus lineatus*) | *Fomes fasciatus*; *Perenniporia martius*; *Phellinus* sp.; unidentified fungi | Kilham and O'Brien (1979) and Cockle et al. (2012) |
| | Black Woodpecker (*Dryocopus martius*) | Unidentified fungi | Hågvar et al. (1990) and Zahner et al. (2012) |
| | Pileated Woodpecker (*Dryocopus pileatus*) | *Fomes fomentarius*; *Phellinus igniarius*; *Postia sericeomollis*; *Sarcodontia pachyodon*; unidentified fungi | Conner et al. (1976), McClelland et al. (1979), Miller et al. (1979), Harris (1983), Keisker (1986), Harestad and Keisker (1989), Parks et al. (1997), McClelland and McClelland (1999), Steeger and Dulisse (2002), Hartwig et al. (2004), Martin et al. (2004), Blanc and Martin (2012), and Edworthy et al. (2012) |
| | Red-bellied Woodpecker (*Melanerpes carolinus*) | Unidentified fungi | Jackson (1976) |
| | Yellow-fronted Woodpecker (*Melanerpes flavifrons*) | *Fomes fasciatus*; unidentified fungi | Cockle et al. (2012) |
| | Lewis's woodpecker (*Melanerpes lewis*) | Unidentified fungi | Raphael and White (1984), Vierling (1997), Linder and Anderson (1998), Saab and Dudley (1998), and Newlon (2005) |
| | White-headed Woodpecker (*Picoides albolarvatus*) | Unidentified fungi | Miller et al. (1979), Raphael and White (1984), Saab and Dudley (1998), and Lorenz et al. (2015) |
| | Black-backed Woodpecker (*Picoides arcticus*) | Unidentified fungi | McClelland et al. (1979), Miller et al. (1979), Raphael and White (1984), Saab and Dudley (1998), Steeger and Dulisse (2002), Martin et al. (2004), and Lorenz et al. (2015) |

**Table 2** continued

| Bird family | Bird species | Fungi[a] | Citations |
|---|---|---|---|
| | Red-cockaded Woodpecker (*Picoides borealis*) | *Coniophora* sp.; *Daedaleopsis confragosa*; *Exidia* sp.; *Peniophora cinera*; *Peniophora incarnata*; *Phlebia brevispora*; *Porodaedalea pini*; *Postia sericemollis*; *Stereum complicatum*; *Trametes versicolor*; unidentified fungi; and more than 40 other putative decay fungi were reported on the birds and in their excavations based on DNA analysis (see Jusino et al. 2014, 2015, 2016 for details) | Steirly (1957), Lay and Russell (1970), Ligon (1971), Conner et al. (1976), Jackson (1977), Conner and Locke (1982), Conner and O'Halloran (1987), Hooper (1988), Hooper et al. (1991), Rudolph and Conner (1991), Conner et al. (1994), Rudolph et al. (1995), Harding (1997), and Jusino et al. (2014, 2015, 2016) |
| | American Three-toed Woodpecker (*Picoides dorsalis*) | Unidentified fungi | McClelland et al. (1979), Miller et al. (1979), Martin et al. (2004), Blanc and Martin (2012), and Edworthy et al. (2012) |
| | Downy Woodpecker (*Picoides pubescens*) | *Fomes fomentarius*; *Phellinus igniarius*; *Sarcodontia pachyodon*; *Trametes versicolor*; unidentified fungi | Conner et al. (1976), McClelland et al. (1979), Keisker (1986), Runde and Capen (1987), Harestad and Keisker (1989), Steeger and Dulisse (2002), Aitken and Martin (2004), Martin et al. (2004), and Blanc and Martin (2012) |
| | Three-toed Woodpecker (*Picoides tridactylus*) | Unidentified fungi | Hågvar et al. (1990), Steeger and Dulisse (2002), and Pakkala et al. (2018) |
| | Hairy Woodpecker (*Picoides villosus*) | *Fomes fomentarius*; *Phellinus igniarius*; *Sarcodontia pachyodon*; unidentified fungi | Kilham (1968), Kilham (1969, 1971), Conner et al. (1976), McClelland et al. (1979), Miller et al. (1979), Raphael and White (1984), Keisker (1986), Harestad and Keisker (1989), Saab and Dudley (1998), Steeger and Dulisse (2002), Aitken and Martin (2004), Martin et al. (2004), Blanc and Martin (2012), Edworthy et al. (2012), and Lorenz et al. (2015) |
| | Grey-headed Woodpecker (*Picus canus*) | Unidentified fungi | Hågvar et al. (1990) |
| | European Green Woodpecker (*Picus viridis*) | Unidentified fungi | Hågvar et al. (1990) and Glue and Boswell (1994) |
| | Red-naped Sapsucker (*Sphyrapicus nuchalis*) | *Fomes* sp.; *Phellinus igniarius*; *Phellinus tremulae*; unidentified fungi | Crockett and Hadow (1975), Daily (1993), Dobkin et al. (1995), Hart and Hart (2001), Steeger and Dulisse (2002), Aitken and Martin (2004), Martin et al. (2004), Losin et al. (2006), Blanc and Martin (2012), and Edworthy et al. (2012) |
| | Red-breasted Sapsucker (*Sphyrapicus ruber*) | Unidentified fungi | Raphael and White (1984) |
| | Williamson's Sapsucker (*Sphyrapicus thyroideus*) | *Phellinus* cf. *tremulae*; unidentified fungi | Crockett and Hadow (1975), McClelland et al. (1979), Miller et al. (1979), and Raphael and White (1984) |
| | Yellow-bellied Sapsucker (*Sphyrapicus varius*) | *Fomes fomentarius*; *Phellinus igniarius*; *Phellinus tremulae*; *Trametes versicolor*; *Trichaptum biforme*; unidentified fungi | Shigo and Kilham (1968), Kilham (1969, 1971), McClelland et al. (1979), Miller et al. (1979), Keisker (1986), Runde and Capen (1987), Harestad and Keisker (1989), and Savignac and Machtans (2006) |
| | White-spotted Woodpecker (*Veniliornis spilogaster*) | Unidentified fungi | Cockle et al. (2012) |

**Table 2** (continued)

| Bird family | Bird species | Fungi[a] | Citations |
|---|---|---|---|
| Semnornithidae | Prong-billed Barbet (*Semnornis frantzii*) | Unidentified fungi | Skutch (1969) |
| Trogonidae | Surucua Trogon (*Trogon surrucura*) | *Ganoderma australe*; *Fomes fasciatus*; *Rigidoporus ulmarius*; unidentified fungi | Cockle et al. (2012) |
| Unknown | Unidentified bird excavated cavities | *Coniophora puteana*; *Fomitopsis pinicola*; *Gloeophyllum sepiarium*; *Neolentinus lepideus*; *Phaeolus schweinitzii*; *Phellinus tremulae*; *Porodaedalea pini*; *Rhodonia placenta*; *Stereum sanguinolentum*; *Wolfiporia cocos*; unidentified fungi | Parks and Bull (1996), Hart and Hart (2001), Aitken and Martin (2004), Witt (2010), Bednarz et al. (2013), and Lõhmus (2016) |

Cavity-excavating bird species and the wood rot fungi they associate with. *Note* The 30 species of birds in this list exhibit excavating behaviours, though some are weakly excavating species. This list does not include bird or mammal species that will secondarily roost or nest inside the cavities made by primary excavators

[a]Fungal names in this table reflect updated nomenclature (as per IndexFungorum and MycoBank) and are not necessarily the same as what appears in the original texts. Methods used by some of the cited authors may not have been reliable; but since there are no voucher specimens for most of these studies, we were unable to confirm or disprove any identifications

sterilised. Small quantities of wood may also be scraped from inside excavations and used for culturing or DNA-based work (Jusino et al. 2014); this technique can reveal very specific taxonomic information about the fungi associated with the decay in cavity trees (Jusino et al. 2014). Several recent studies used these minimally invasive techniques and detected rot (Zahner et al. 2012, Lorenz et al. 2015) or fungal species (Jusino et al. 2014, 2015, 2016) that the more traditional standard observational techniques would likely have missed.

We found studies reporting 30 cavity-excavating bird species that form associations with fungal wood rots to varying degrees (Table 2). These associations have been primarily shown among members of the woodpecker family (Picidae). Many of these studies provide support for the tree selection hypothesis, but the fungi the birds are selecting and the mechanisms behind tree selection are largely unknown. Some authors have suggested that cavity-excavating birds use fungal fruiting bodies or visual cues to select foraging and excavation sites (Savignac and Machtans 2006; Witt 2010; Zahner et al. 2012 O'Daniels et al. 2017). Others have argued that visual detection of fungi to select excavation sites is unlikely. Rudolph et al. (1995) tested this specifically with red-cockaded woodpeckers and concluded that they do not use fruiting bodies to select excavation sites. It is possible that birds use olfactory, tactile, auditory and other sensory cues to detect decayed wood (Jusino et al. 2016).

Many primary excavators only use cavities for one season. Some notable exceptions to this are red-cockaded woodpeckers and acorn woodpeckers (*Melanerpes formicivorus*). Both of these species are cooperative breeders, live in family groups, maintain territories year-round, and use their cavities for nightly roosting. Cavities made by primary excavators also serve as important roosts and nests for numerous other "secondary" cavity users (both birds and mammals) (McClelland et al. 1979; Short 1979; Harestad and Keisker 1989; Daily et al. 1993; Jackson and Jackson 2004; Martin et al. 2004; Bednarz et al. 2004; Nielsen et al. 2007; Blanc and Walters 2008; Witt 2010; Cockle et al. 2011). Because many species depend on old or injured trees with cavities, forest stands with diverse cavity-bearing trees are important for maintaining forest biodiversity.

Even though many organisms depend on trees with decay, management strategies often favour the removal of trees with signs of rot to limit the spread of fungal rot within managed timber. The continued loss of old growth trees negatively impacts the primary cavity-nesting birds and the many secondary cavity dwellers (Flack 1976; Bull et al. 1980; Miller and Miller 1980; Aitken and Martin 2004; Cornelius et al. 2008; Witt 2010; Cockle et al. 2012; Wesołowski 2012). Some cavity-excavating bird species

and individuals compete for suitable cavity trees (Kilham 1969). The loss of old and decay-prone trees has contributed to the decline and even extinction of some species (Allen and Kellogg 1937; Conner and Rudolph 1991; Lammertink and Estrada 1995; Harding 1997). In an attempt to restore habitat and create future nesting cavities, live trees have been experimentally inoculated with *Fomitopsis pinicola* (Bednarz et al. 2013); but further experimentation is still needed to fully understand the effectiveness of this method.

Much of the research on associations between fungi and cavity-dwelling animals has been conducted in temperate systems in North America and Europe. Increased research attention in other areas could help to inform international conservation approaches. Cockle et al. (2011) estimated that in North America, excavators produced 77% of cavities used by non-excavators; the rate was 27% in Eurasia and 25% in South America. It should be noted that these percentages may be tenuous in some areas due to the limited number of studies in South America and Africa. In regions where woodpecker/primary excavator populations are small or absent (e.g. Australia, New Guinea, New Zealand and Madagascar), most non-excavating cavity-nesting birds depend on saprotrophic fungi for rotting out cavities (Gibbs et al. 1993; Steeger and Dulisse 2002; Cornelius et al. 2008; Cockle et al. 2011; Wesołowski 2012; Cockle et al. 2012). A more thorough understanding of these associations and dependencies could be reached if future studies were to include molecular community characterisation of the fungi associated with non-excavating cavity nesters.

It is unclear to what extent birds disperse spores of the fungi found in their excavations. Some birds are vectors of fungal pathogens that lead to tree mortality (Heald and Studhalter 1913, 1914), and some disperse fungi such as yeasts and filamentous fungi (Warner and French 1970; Farris et al. 2004; Alfonzo et al. 2013; Francesca et al. 2013; Jusino et al. 2016); however, the dispersal of decay fungi has been less thoroughly studied (but see Jusino et al. 2016). Skutch (1969) observed secondary cavity nesters using a cavity directly below a bracket fungus, presumably collecting spores on their plumage. In a two-year field experiment using molecular sampling techniques, Jusino et al. (2016) concluded that red-cockaded woodpeckers disperse many fungi into their excavations, including wood decay fungi. Many fungi are likely being dispersed into trees by the birds' foraging activities (Farris et al. 2004). For example, sapsuckers' behaviour of boring sap holes in healthy trees is an ideal mechanism for the dispersal and/or entry of decay fungi. This likely allows some fungi to enter the heartwood of other trees, but further study is needed (Jusino et al. 2016).

Some birds may disperse fungi in their faeces. Woodpeckers consume fungus-carrying insects (Edworthy et al. 2011; Watson and Shaw 2018), and as young woodpeckers mature, nest cleanliness generally declines; by fledging time, faecal material and other debris have often built up inside the cavity (Jackson and Jackson 2004). Thus, it is possible that the birds could be spreading fungi from the nesting cavity through the tree via their scats.

There is little known about what—if any—health benefits the primary or secondary cavity dwellers get from fungi in their cavities. The acaropathogenic (mite killing) fungus *Acaromyces ingoldii* has been detected in some red-cockaded woodpecker cavities and may benefit these birds by parasitizing mites and other ectoparasites in their nests (Jusino 2014; Jusino et al. 2015). The chemical compounds produced by other cavity-associated fungi may also impact bird health. An example is the fungus *Fomes fomentarius*, which is found in the nest trees of at least six primary cavity-excavating bird species (Table 2). Due to the historical significance of this polypore in folk medicine, its bioactivity has been better studied than many fungi associated with bird cavities. *Fomes fomentarius* contains a range of chemicals, including antibacterial (Kolundžić et al. 2016), antimicrobial (Suay et al. 2000), antiviral (Aoki et al. 1993) and cytotoxic (Kolundžić et al. 2016) compounds. It also produces volatiles that attract insects (Fäldt et al. 1999). These and related studies are part of the "bioprospecting" research for human medical applications, so they unfortunately do not directly evaluate the impacts that these compounds have on wildlife that cohabitate with fungi. Similar compounds are found in other fungal species reported from cavities, but it is also unclear if these compounds have an impact on wildlife. There has been some research into the health consequences of nesting material for birds (Clark and Mason 1985, and see discussion in following section), but this has not been studied in relation to cavity-dwelling species. Further testing is needed, but based on clinical studies, the presence of mycelia from wood-decomposing fungi in nest cavities likely plays a beneficial role in the success of cavity-dwelling animals and may directly benefit their health.

## Bird-fungal associations among bowerbirds and open nest building birds

Construction of bowers by bowerbirds (Ptilonorhynchidae) has been widely recognised as one of the more charismatic examples of sexual selection among vertebrates. Extensive lists have been compiled of the many colourful objects collected by these Australian and New Guinean birds, including a man's glass eyeball, bones, car keys, leaves, flowers, plastic and fungi (Chisholm 1929; Marshall 1954;

Elliott and Marshall 2016). Because these birds seek certain coloured objects to attract mates, a diversity of colourful fungi meet their colour criteria; consequently, fungi are widely used for bowerbird bower ornamentation. Elliott and Marshall (2016) report at least three bowerbird species using fungi in bowers and propose that satin bowerbirds (*Ptilonorhynchus violaceus*) may contribute to the dispersal of the colourful non-native mushroom, *Lepista nuda*. This phenomenon is reported less frequently than it actually occurs, and when noted, the researchers rarely identify the fungi even to order. We have encountered video footage and images on the internet of bowerbirds with a diversity of fungi in their bowers (e.g. BBC's *The Vogelkop Bowerbird: Nature's Great Seducer*, Attenborough). In December of 2018, the first author encountered a satin bowerbird near Monga National Park in New South Wales, Australia, that had collected fruiting bodies of a non-native fungus (*Rhizopogon* sp.) from a nearby pine plantation and placed them near its bower. Bowerbirds' use of fungi likely plays a role in the dispersal of both native and non-native fungi and may apply selective pressures toward fungal colours (Elliott and Marshall 2016).

Some birds inadvertently disperse fungi during nest construction. For example, mud used by swallows has been found to contain spores of soil fungi in the family Endogonaceae (McIlveen and Cole 1976). Other birds deliberately select fungi as a component in nest construction. Many groups of fungi form filament structures (rhizomorphs) that are often used for trapping organic material in the canopy (Hedger et al. 1993; Koch et al. 2018). The rhizomorphs of the widespread fungal genera *Armillaria*, *Brunneocorticium, Cylindrobasidium, Gymnopus* and *Marasmius* have been reported as components of the nests of at least 176 different open-nesting bird species in 37 families (Table 3); of these, *Marasmius* is by far the most commonly reported fungal genus. Gómez-García et al. (2014) also reported the genus *Crinipellis* to be used as nesting material by an unidentified bird in Mexico. As rhizomorphs rarely have fruiting bodies, it is difficult to use morphology alone to determine their taxonomy. Using DNA analysis of the rhizomorphs found in bird nests in the cloud forests of Mexico, César et al. (2018) determined the presence of an array of species of fungi; however, they provide little information as to which species of fungi and birds are associated with one another. The only evidence we have found of certain bird species selecting particular species of rhizomorphs over others is among the West African species of bristlebills (*Bleda* spp.). Brosset (1974) reported that one of the best ways to distinguish the very similar nests of *B. eximia* and *B. syndactyla* is that *B. syndactyla* uses rhizomorphs twice the diameter (1 mm) of the other (0.5 mm). Further research is needed to be sure, but it is likely that there are other cases of certain bird species targeting the rhizomorphs of only particular species or genera of fungi. Many nests are found after the builder has vacated the nest, and DNA-based molecular techniques could perhaps be used in these cases to determine who the nest user was.

Pliable, hair-like rhizomorphs are an ideal material for nest construction because they have very strong tensile strength; they are less water absorptive than most other naturally occurring fibres, which can help to maintain nestling fitness (Freymann 2008; Koch et al. 2018). Fungi in the genus *Marasmius* also have antibacterial, antifungal and anti-tumor properties that may improve the health and success of nestling birds (Melin et al. 1947; Anke et al. 1980; Rosa et al. 2009; Aubrecht et al. 2013). It is possible that some birds choose different fungal species due to the presence of different volatiles or other bioactive compounds. It is also possible that in areas of high rhizomorph use, it is simply the best nest-building material available.

Assessing the importance of rhizomorphs as nesting material is difficult because this behaviour has not been systematically studied; but in some situations, birds have built nests almost entirely out of rhizomorphs (Botero 2001; Greeney 2004). In some cases, the fungal material has been shown to help secure nests to trees by bonding them with mycelium (Greeney and Sheldon 2008). Rhizomorphs are undoubtedly a far more common nesting material than is generally reported. Due to the difficulties in identifying rhizomorphs and the obscure nature of the material, many studies we read for this review report unidentified/misidentified materials; but based on descriptions, we believe these likely represent rhizomorphs. McFarland and Rimmer (1996) and Chatellenaz and Ferraro (2000) also report many studies likely referring to rhizomorphs, but they list the material under a variety of descriptive names. For the sake of accuracy in Table 3, we have only cited studies that list fungal rhizomorphs or reports that give descriptions specific enough for us to feel confident in identifying materials from descriptions or plates.

There are still too few studies to determine how much fungi benefit from being used as nesting material. In a study of 15 streak-backed oriole (*Icterus pustulatus*) nests, Freymann (2008) concluded that *Marasmius* rhizomorphs were dead and did not grow after being used as nesting material. Hedger et al. (1993) reported that apical regeneration of rhizomorphs occurs but that in situations where more than 10 mm had been removed, they failed to regenerate. This suggests that among some rhizomorph-forming fungi, there is a limit on the length that can be removed while still allowing for regeneration. Given the diversity of fungi that produce rhizomorphs, this limitation likely varies depending on the fungal species involved. Hummingbirds have been reported to use *Marasmius*

**Table 3** Open-nesting birds and their use of fungal nesting material

| Bird family | Bird name | Species of rhizomorph[a] | Citations |
|---|---|---|---|
| Cardinalidae | Tanager (*Chlorothraupis olivacea* or *C. carmioli*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Black-and-white Tanager (*Conothraupis speculigera*) | Black fungal rhizomorphs, *Marasmius* sp. | Greeney et al. (2006), Ingels (2007), and Aubrecht et al. (2013) |
| | Blue-black Grosbeak (*Cyanocompsa cyanoides*) | Fungal strands | Skutch (1969) |
| | Black-cheeked Ant Tanager (*Habia atrimaxillaris*) | *Marasmius* sp.; rhizomorphs | Huber et al. (2008) and Sandoval and Gallo (2009) |
| | Sooty Ant Tanager (*Habia gutturalis*) | *Marasmius* sp. | Willis (1961) |
| | Red-crowned Ant Tanager (*Habia rubica*) | *Marasmius* sp. | Willis (1961) and Foster and Escobar (1989) |
| Certhiidae | Brown Creeper (*Certhia americana*) | *Marasmius androsaceus* | Aubrecht et al. (2013) [possibly an erroneous citation of McFarland and Rimmer (1996)] |
| Conopophagidae | Chestnut-belted Gnateater (*Conopophaga aurita*) | Blackish-biolaceous fungus fibers | del Hoyo et al. (2003) and citations within |
| | Black-cheeked Gnateater (*Conopophaga melanops*) | *Marasmius* sp. | Sick (1957) |
| Corvidae | Common Green Magpie (*Cissa chinensis*) | *Gymnopus* sp. or *Marasmius* sp. | Boyce (2018) |
| Cotingidae | Amazonian Umbrellabird (*Cephalopterus ornatus*) | White fungus covered twigs | Greeney and Sheldon (2008) |
| | Turquoise Cotinga (*Cotinga ridgwayi*) | Rhizomorphs | Skutch (1969) |
| | Bare-necked Fruitcrow (*Gymnoderus foetidus*) | White fungus coated twigs, *Brunneocorticium corynecarpon* | Greeney and Gelis (2008) and Koch et al. (2018) |
| Dicruridae | Hair-crested Drongo (*Dicrurus hottentottus*) | *Gymnopus* sp. or *Marasmius* sp. | Boyce (2018) |
| Estrildidae | Blue-faced Parrotfinch (*Erythrura trichroa*) | *Marasmius equicrinus* | Marshall (1948) |
| Eurylaimidae | Black-and-yellow Broadbill (*Eurylaimus ochromalus*) | Fungal mycelia | del Hoyo et al. (2003) and citations within |
| | Black-and-red Broadbill (*Cymbirhynchus macrorhynchos*) | Fungal hyphae; *Marasmius* sp. | del Hoyo et al. (2003), citations within; Aubrecht et al. (2013) |
| | Silver-breasted Broadbill (*Sterilophus lunatus*) | Fungal hyphae | del Hoyo et al. (2003) and citations within |
| | African Broadbill (*Smithornis capensis*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within |
| | Broadbill (*Smithornis sharpei*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within |
| | Rufous-sided Broadbill (*Smithornis rufolateralis*) | Unidentified; *Marasmius* sp. | Chapin (1953), del Hoyo et al. (2003) and citations within |
| Fringillidae | Scrub Euphonia (*Euphonia affinis*) | Unidentified | Gómez (1983) |
| | Purple-throated Euphonia (*Euphonia chlorotica*) | *Marasmius* sp. | Sick (1957) |
| | Purple Finch (*Carpodacus purpureus*) | *Marasmius androsaceus* | Aubrecht et al. (2013) [possibly an erroneous citation of McFarland and Rimmer (1996)] |
| Formicariidae | Short-tailed Antthrush (*Chamaeza campanisona*) | Fungal rhizomorphs | Cadena et al. (2000) |
| | Rufous-tailed Antthrush (*Chamaeza ruficauda*) | Fungal rhizomorphs | Cadena et al. (2000) |
| Furnariidae | Pink-legged Graveteiro (*Acrobatornis fonsecai*) | *Marasmius* sp. | Whitney et al. (1996) |
| | Ruddy Foliage-gleaner (*Clibanornis rubiginosus*) | *Marasmius* sp.; fungal rhizomorphs | Zyskowski and Prum (1999), del Hoyo et al. (2003) and citations within |
| | Tawny-winged Woodcreeper (*Dendrocincla anabatina*) | Fungal rhizomorphs | Skutch (1969) |

**Table 3** continued

| Bird family | Bird name | Species of rhizomorph[a] | Citations |
|---|---|---|---|
| | Wedge-billed Woodcreeper (*Glyphorynchus spirurus*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Foliage-gleaner (*Hylocryptus* sp.) | *Marasmius* sp. | Zyskowski and Prum (1999) |
| | Foliage-gleaner (*Philydor* sp.) | *Marasmius* sp. | Zyskowski and Prum (1999) |
| | Streak-breasted Treehunter (*Thripadectes rufobrunneus*) | *Marasmius* sp. | Zyskowski and Prum (1999) |
| | Ovenbird (*Xenops* sp.) | *Marasmius* sp. | Zyskowski and Prum (1999) |
| Grallariidae | Ochre-breasted Antpitta (*Grallaricula flavirostris*) | Black rhizomorphs | Holley et al. (2001), del Hoyo et al. (2003) and citations within |
| | Thrush-like Antpitta (*Myrmothera campanisona*) | Hyphae | del Hoyo et al. (2003) and citations within |
| Icteridae | Yellow-billed Cacique (*Amblycercus holosericeus*) | Unidentified | Gómez (1983) |
| | Golden-winged Cacique (*Cacicus chrysopterus*) | *Marasmius* sp. and *M. crinisequi* | Sick (1957), Wright and Ferraro (1986), and Chatellenaz and Ferraro (2000) |
| | Red-rumped Cacique (*Cacicus haemorrhous*) | *Marasmius crinisequi* | Wright and Ferraro (1986) |
| | Ecuadorian cacique (*Cacicus sclateri*) | *Marasmius* sp. | Botero (2001) |
| | Streak-backed Oriole (*Icterus pustulatus*) | *Marasmius* sp. | Freymann (2008) |
| | Crested Oropendola (*Psarocolius decumanus*) | *Marasmius* sp. | Goeldi (1897) |
| | Chestnut-headed Oropendola (*Psarocolius wagleri*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| Leiothrichidae | Red-billed Leiothrix (*Leiothrix lutea*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| Meliphagidae | Short-bearded Melidectes (*Melidectes nouhuysi*) | Unidentified | Rand (1942) |
| Monarchidae | Black-naped Monarch (*Hypothymis azurea*) | *Marasmius* sp. | Chen et al. (2010) |
| | Vanikoro Monarch (*Mayrornis schistaceus*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Black Monarch (*Symposiachrus axillaris*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Hooded Monarch (*Symposiachrus manadensis*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Spectacled Monarch (*Symposiachrus trivirgatus*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| Muscicapidae | Alethe (*Alethe* spp.) | *Marasmius* sp. | Brosset (1974) |
| | Flycatchers (*Fraseria* spp.) | *Marasmius* sp. | Brosset (1974) |
| | Forest Robin (*Stiphrornis erythrothorax*) | *Marasmius* sp. | Brosset (1974) |
| Nectariniidae | Brown-throated Sunbird (*Anthreptes malacensis*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Olive Sunbird (*Cyanomitra olivacea*) | *Marasmius* sp. | Hockey et al. (2005) |
| Nesospingidae | Puerto Rican Tanager (*Nesospingus speculiferus*) | Unidentified | Perez-Rivera (1993) |
| Nicatoridae | Western nicator (*Nicator chloris*) | Mycelium | Brosset (1974) |
| Pachycephalidae | Rusty Pitohui (*Pseudorectes ferrugineus*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| Paradisaeidae | Long-tailed Paradigalla (*Paradigalla carunculata*) | *Marasmius* sp. | Aubrecht et al. (2013) |

**Table 3** continued

| Bird family | Bird name | Species of rhizomorph[a] | Citations |
|---|---|---|---|
| Passerellidae | Sooty-faced Finch (*Arremon crassirostris*) | Unidentified | Young and Zook (1999) |
| | Pectoral Sparrow (*Arremon taciturnus*) | *Marasmius* sp. | Sick (1957) |
| | Dark-eyed Junco (*Junco hyemalis*) | *Marasmius androsaceus* | Aubrecht et al. 2013 [possibly an erroneous citation of McFarland and Rimmer (1996)] |
| | White-throated Sparrow (*Zonotrichia albicollis*) | *Marasmius androsaceus* | Aubrecht et al. (2013) [possibly an erroneous citation of McFarland and Rimmer (1996)] |
| Parulidae | Mourning Warbler (*Geothlypis philadelphia*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Magnolia Warbler (*Setophaga magnolia*) | *Marasmius androsaceus* | McFarland and Rimmer (1996) |
| | Ovenbird (*Seiurus aurocapilla*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Yellow-rumped Warbler (*Setophaga coronata*) | *Marasmius androsaceus* | McFarland and Rimmer (1996) |
| | Blackpoll Warbler (*Setophaga striata*) | *Marasmius androsaceus* | McFarland and Rimmer (1996) |
| | Bachman's Warbler (*Vermivora bachmanii*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| Pellorneidae | Puff-throated Babbler (*Pellorneum ruficeps*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Sulawesi Babbler (*Trichastoma celebense*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| Pipridae | Golden-headed Manakin (*Ceratopipra erythrocephala*) | *Marasmius* sp. | Tostain (1988) |
| | Red-capped Manakin (*Ceratopipra mentalis*) | Black fungal filaments | Skutch (1969) |
| | Swallow-tailed Manakin (*Chiroxiphia caudata*) | *Marasmius* sp. | Sick (1957) |
| | Lance-tailed Manakin (*Chiroxiphia lanceolata*) | *Marasmius* sp. | Foster (1976) |
| | Long-tailed Manakin (Chiroxiphia linearis) | *Marasmius* sp. | Foster (1976) |
| | Orange-collared Manakin (*Manacus aurantiacus*) | Rhizomorphs; *Marasmius* sp. | Skutch (1969) and Aubrecht et al. (2013) |
| | Wire-tailed Manakin (*Pipra filicauda*) | Rhizomorphs | Hidalgo et al. (2008) |
| | White-crowned Manakin (*Pseudopipra pipra*) | *Marasmius* sp. | Tostain (1988) |
| | Javan Banded Pitta (*Hydrornis guajanus*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| Pycnonotidae | Sombre Greenbul (*Andropadus importunus*) | *Marasmius* sp. | Brosset (1974) |
| | Green-tailed Bristlebill (*Bleda eximius*) | Unidentified; *Marasmius* sp. | Chapin (1953) and Brosset (1974) |
| | Red-tailed Bristlebill (*Bleda syndactylus*) | *Marasmius* sp. | Brosset (1974) |
| | Western Bearded Greenbul (*Criniger barbatus*) | Fungus | Brosset (1974) |
| | Brown-eared Bulbul (*Hypsipetes amaurotis*) | *Cylindrobasidium argenteum*, *Marasmius* sp. | Kusunoki et al. (1997) |
| | Icterine Greenbul (*Phyllastrephus icterinus*) | *Marasmius* sp. | Bates (1927) |
| Rhinocryptidae | Silvery-fronted Tapaculo (*Scytalopus argentifrons*) | *Marasmius* sp. | Young and Zuchowski (2003) |
| Thamnophilidae | White-bearded Antshrike (*Biatas nigropectus*) | "Fungal strands (seemingly of *Merasmius*)" [probably a typo for *Marasmius*] | del Hoyo et al. (2003) and citations within |

**Table 3** continued

| Bird family | Bird name | Species of rhizomorph[a] | Citations |
|---|---|---|---|
| | Dusky Antbird (*Cercomacroides tyrannina*) | Fungal filaments; unidentified; *Marasmius* sp. | Skutch (1969), Morton et al. (2000), del Hoyo et al. (2003) and citations within; Aubrecht et al. (2013) |
| | Fasciated Antshrike (*Cymbilaimus lineatus*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Scaled Antbird (*Drymophila squamata*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within |
| | Plain Antvireo (*Dysithamnus mentalis*) | Fungal filaments; *Marasmius* sp. | Skutch (1969), del Hoyo et al. (2003) and citations within; Aubrecht et al. (2013) |
| | Bicolored Antvireo (*Dysithamnus occidentalis*) | Black fungal filaments; Unidentified | del Hoyo et al. (2003) and citations within; Greeney (2004) |
| | Checker-throated Antwren (*Epinecrophylla fulviventris)* | Blackish-brown fungal filaments | del Hoyo et al. (2003) and citations within |
| | Brown-bellied Antwren (*Epinecrophylla gutturalis*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within |
| | White-cheeked Antbird (*Gymnopithys leucaspis*) | Rhizomorphs | del Hoyo et al. (2003) and citations within |
| | Large-billed Antwren (*Herpsilochmus longirostris*) | *Marasmius* sp. | Straube et al. (1992), del Hoyo et al. (2003) and citations within |
| | Pectoral Antwren (*Herpsilochmus pectoralis*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Caatinga Antwren (*Herpsilochmus sellowi*) | *Marasmius* sp. | Silva et al. (2008) |
| | Spotted Antbird (*Hylophylax naevioides*) | Fungal hyphae; rhizomorphs | Skutch (1946), Skutch (1969), del Hoyo et al. (2003) and citations within |
| | Spot-backed Antbird (*Hylophylax naevius*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within |
| | Guianan Warbling Antbird (*Hypocnemis cantator*) | Rhizomorphs | del Hoyo et al. (2003) and citations within |
| | Dot-winged Antwren (*Microrhopias quixensis*) | Fungal hyphae | Skutch (1969) |
| | Ferruginous-backed Antbird (*Myrmoderus ferrugineus*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within |
| | Scalloped Antbird (*Myrmoderus ruficauda*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within; Silva et al. (2008) and citations within |
| | Black-throated Antbird (*Myrmophylax atrothorax*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within |
| | Wing-banded Antbird (*Myrmornis torquata*) | Rhizomorphs | del Hoyo et al. 2003 and citations within |
| | White-flanked Antwren (*Myrmotherula axillaris*) | *Marasmius* sp.; fungal rhizomorphs | Skutch (1946), Skutch (1969), Sick (1957), del Hoyo et al. (2003) and citations within; Chaparro-Herrera and Ruiz-Ovalle (2014) (and citations within) |
| | Cherrie's Antwren (*Myrmotherula cherriei*) | *Marasmius* sp. | Chaparro-Herrera and Ruiz-Ovalle (2014) (and citations within) |
| | Long-winged Antwren (*Myrmotherula longipennis*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within, Chaparro-Herrera and Ruiz-Ovalle (2014) (and citations within) |
| | Amazonian Streaked Antwren (*Myrmotherula multostriata*) | White fungal rhizomophs | del Hoyo et al. (2003) and citations within; Chaparro-Herrera and Ruiz-Ovalle (2014) (and citations within) |
| | Slaty Antwren (*Myrmotherula schisticolor*) | Fungal strands; black fungal rhizomorphs | Skutch (1969), del Hoyo et al. (2003) and citations within |
| | Guianan Streaked Antwren (*Myrmotherula surinamensis*) | *Marasmius* sp. | Sick (1957) |

**Table 3** continued

| Bird family | Bird name | Species of rhizomorph[a] | Citations |
|---|---|---|---|
| | Unicolored Antwren (*Myrmotherula unicolor*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within; Chaparro-Herrera and Ruiz-Ovalle (2014) (and citations within) |
| | Ocellated Antbird (*Phaenostictus mcleannani*) | *Marasmius* sp. | Buehler et al. (2004) |
| | Chestnut-backed Antbird (*Poliocrania exsul*) | Blackish fungal hyphae; rhizomorphs; fungal Filments | Skutch (1969), Willis and Oniki (1972), del Hoyo et al. (2003) and citations within |
| | Star-throated Antwren (*Rhopias gularis*) | *Marasmius* sp.; black fungal hyphae | del Hoyo et al. (2003) and citations within; Perrella et al. (2015) |
| | Orange-bellied Antwren (*Terenura sicki*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within |
| | Russet Antshrike (*Thamnistes anabatinus*) | Dark fungal rhizomorphs | del Hoyo et al. (2003) and citations within |
| | Dusky-throated Antshrike (*Thamnomanes ardesiacus*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within |
| | Cinereous Antshrike (*Thamnomanes caesius*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within |
| | Amazonian Antshrike (*Thamnophilus amazonicus*) | Black rhizomorph threads similar to horsehair | del Hoyo et al. (2003) and citations within |
| | Black-crowned Antshrike (*Thamnophilus atrinucha*) | Shiny rhizomorphs, *Marasmius* sp. | del Hoyo et al. (2003) and citations within; Silva et al. (2008) and citations within |
| | Collared Antshrike (*Thamnophilus bernardi*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Black-hooded Antshrike (*Thamnophilus bridgesi*) | Fungal filaments | Skutch (1969) |
| | Variable Antshrike (*Thamnophilus caerulescens*) | Rhizomorphs | del Hoyo et al. (2003) and citations within |
| | Barred Antshrike (*Thamnophilus doliatus*) | Fungal rhizomorphs | del Hoyo et al. (2003) and citations within |
| | Band-tailed Antshrike (*Thamnophilus melanothorax*) | Black fungal rhizomorphs and white nodulous mycelia | Zyskowski et al. (2008) |
| | Mouse-colored Antshrike (*Thamnophilus murinus*) | Black and brown rhizomorphs | del Hoyo et al. (2003) and citations within |
| | Chestnut-backed antshrike (*Thamnophilus palliatus*) | Fungus, *Marasmius* sp. | del Hoyo et al. (2003) and citations within; Aubrecht et al. (2013) |
| | Northern Slaty Antshrike (*Thamnophilus punctatus*) | Black horsehair-like rhizomorphs and brown rhizomorphs | del Hoyo et al. (2003) and citations within |
| | Plain-winged Antshrike (*Thamnophilus schistaceus*) | Fungus-whitened twigs | del Hoyo et al. (2003) and citations within |
| | Rufous-winged Antshrike (*Thamnophilus torquatus*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within; Silva et al. (2008) and citations within |
| | Common Scale-backed Antbird (*Willisornis poecilinotus*) | *Marasmius* sp. | del Hoyo et al. (2003) and citations within |
| Thraupidae | Black-and-yellow Tanager (*Chrysothlypis chrysomelas*) | fungal rhizomorphs | Marin and Schmitt (1991) |
| | Hooded Tanager (*Nemosia pileata*) | *Marasmius* sp. | Sick (1957) |
| | Nicaraguan Seed Finch (*Oryzoborus nuttingi*) | *Marasmius crinisiqui* | Stiles (1984) |
| | Brazilian Tanager (*Ramphocelus bresilius*) | *Marasmius* sp. | Sick (1957) |
| | Cherrie's Tanager (*Ramphocelus passerinii costaricensis*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Variable Seedeater (*Sporophila corvina*) | *Marasmius sarmentosus* | Gross (1952) |
| | Ruby-crowned Tanager (*Tachyphonus coronatus*) | *Marasmius* sp. | Sick (1957) |
| | Burnished-buff Tanager (*Tangara cayana*) | *Marasmius* sp. | Sick (1957) |
| | Paradise Tanager (*Tangara chilensis*) | *Brunneocorticium corynecarpon* | Wood et al. (1992) |

**Table 3** continued

| Bird family | Bird name | Species of rhizomorph[a] | Citations |
|---|---|---|---|
| | Blue-necked Tanager (*Tangara cyanicollis*) | *Marasmius* sp. | Sick (1957) |
| | Brassy-breasted Tanager (Tangara desmaresti) | Fungal rhizomorphs | Gonzaga and Castiglioni (2006) |
| | Silver-throated Tanager (*Tangara icterocephala*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Sayaca Tanager (*Thraupis sayaca*) | *Marasmius* sp. | Sick (1957) |
| | Green-and-gold Tanager (*Tangara schrankii*) | Fungal rhizomorphs | Kirwan (2011) |
| Timaliidae | Not reported | *Marasmius* sp. | Brosset (1974) |
| Tityridae | Whiskered Myiobius (*Myiobius barbatus*) | Dark fungal rhizomorphs | Greeney and Gelis (2008) |
| | Brown-winged Schiffornis (*Schiffornis turdina*) | Black fungal filaments | Skutch (1969) |
| Trochilidae | Green-breasted Mango (*Anthracothorax prevostii*) | Unidentified | Gómez (1983) |
| | Rufous-breasted Hermit (*Glaucis hirsutus*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Hummingbirds (Trochilidae) | *Marasmius nigrobrunneus* | Hedger (1990) |
| Troglodytidae | Niceforo's Wren (*Thryophilus nicefori*) | *Marasmius* sp. | Valderrama et al. (2007) |
| Turdidae | Bicknell's thrush (*Catharus bicknelli*) | *Marasmius androsaceus*; Unidentified | Wallace 1939 and McFarland and Rimmer (1996) |
| | Veery (*Catharus fuscescens*) | *Armillaria mellea* | Heckscher et al. (2014) |
| | Swainson's Thrush (*Catharus ustulatus*) | *Marasmius androsaceus* | McFarland and Rimmer (1996) |
| Tyrannidae | Bright-rumped Attila (*Attila spadiceus*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Tropical Pewee (*Contopus cinereus*) | *Marasmius* sp. | Sick (1957) |
| | Highland Elaenia (*Elaenia obscura*) | *Marasmius* sp. | Sick (1957) |
| | Yellow-bellied Flycatcher (*Empidonax flaviventris*) | *Marasmius androsaceus* | McFarland and Rimmer (1996) |
| | Drab-breasted Bamboo Tyrant (*Hemitriccus diops*) | Fungal rhizomorphs | Kirwan and Whittaker (2009) |
| | Brown-breasted Bamboo Tyrant (*Hemitriccus obsoletus*) | *Marasmius* sp. | Bencke et al. (2001) |
| | White-winged Black Tyrant (*Knipolegus aterrimus*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Ochre-bellied Flycatcher (*Mionectes oleagineus*) | *Gymnopus nidus-avis* | César et al. (2018) |
| | Grey-hooded Flycatcher (*Mionectes rufiventris*) | *Marasmius* sp. | Aguilar et al. (2000) |
| | Flycatcher (*Myiarchus ferox* or *M. panamensis*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Bran-colored Flycatcher (*Myiophobus fasciatus*) | Fungal rhizomorphs; *Marasmius* sp. | Greeney et al. (2005) and Aubrecht et al. (2013) |
| | Cocos flycatcher (*Nesotriccus ridgwayi*) | *Marasmius crinisiqui* | Sherry (1986) |
| | Black-capped Piprites (*Piprites pileata*) | *Marasmius* sp. | Cockle et al. (2008) |
| | White-throated Spadebill (*Platyrinchus mystaceus*) | *Marasmius* sp. | Sick (1957) |
| | Eye-ringed Flatbill (*Rhynchocyclus brevirostris*) | *Marasmius* sp. | Aubrecht et al. (2013) |
| | Common Tody-Flycatcher (*Todirostrum cinereum*) | *Marasmius* sp. | Solano-Ugalde et al. (2007) |
| | Yellow-olive Flycatcher (*Tolmomyias sulphurescens*) | *Marasmius* sp. | Sick (1957), Gómez (1983), and Chatellenaz and Ferraro (2000) |

**Table 3** (continued)

| Bird family | Bird name | Species of rhizomorph[a] | Citations |
|---|---|---|---|
| Vangidae | Blue Vanga (*Cyanolanius madagascarinus*) | *Marasmius* sp. | Aubrecht et al. (2013) |

Open-nesting birds and their use of fungal material for nesting. There are 176 bird species in 37 families reported to use fungal rhizomorphs as nesting material. *Note* Much of the data published by Aubrecht et al. (2013) is cited in their references as personal communications. When multiple studies reported the use of rhizomorphs for a single bird species, Aubrecht et al. (2013) were unclear in specifying which fungal species was documented by which original source. We also think that they may have misinterpreted data published by McFarland and Rimmer (1996), so we have made note of this possible mistake in this table; we recommend that any researchers interested in rhizomorph use by birds compare the data presented in McFarland and Rimmer (1996) with what is published in Aubrecht et al. (2013)

[a]Fungal names in this table reflect updated nomenclature (as per IndexFungorum and MycoBank) and are not necessarily the same as what appears in the original texts. Methods used by some of the cited authors may not have been reliable; but since there are no voucher specimens for most of these studies, we were unable to confirm or disprove any identifications

*nigrobrunneus* as a nesting material, and the rhizomorphs in use were later reported to produce fruiting bodies (Hedger 1990). This suggests that some hummingbirds may play a role in the dispersal of litter decay fungi in Neotropical forests. Rhizomorphs in wire-tailed manakin (*Pipra filicauda*) nests have been reported to re-sprout after the nests have been inactive for 7–10 days (Hidalgo et al. 2008). In North America, birds that use *M. androsaceus* rhizomorphs as nesting material sometimes leave the fruiting bodies attached (McFarland and Rimmer 1996). The birds' transportation of *M. androsaceus* fruiting bodies and use of them in nest construction would inadvertently lead to the dispersal of spores. *Gymnopus nidus-avis* was given its specific epithet because it was found to be used in bird nests (César et al. 2018), but whether or not birds play a role in its dispersal is currently unknown. Koch et al. (2018) evaluated the taxonomy and ecology of the tropical rhizomorph-forming fungus *Brunneocorticium corynecarpon*, which has never been reported to form fruiting bodies; they hypothesize that it might be reliant on bird dispersal, but they were not able to determine whether or not bird-collected rhizomorphs were viable.

Birds may also spread fungi via non-rhizomorphic mycelia. In Japan, birds have been shown to disperse the corticioid macrofungus *Cylindrobasidium argenteum* through nesting material; the fungus spread from one tree to another through direct contact, and in several cases the fungus spread from nests composed of infected twigs to the nests' host trees (Kusunoki et al. 1997). In Gabon, nests of several bird species are particularly flimsy and rely on mycelia growing out from their half-rotted twigs and onto the host trees; if these nests last even a few days after being built, the mycelia have enough time to grow and effectively "glue" the nests to their supports (Brosset 1974). Brosset reported that incorporation of half-rotted twigs was not a chance event but a deliberate selection; also noted was that within a given bird genus, one species used half-rotted twigs and another did not. Greeney and Sheldon (2008) reported "a film of white fungus" that glued nesting material together. The nest they studied was not glued to the host tree, but perhaps not enough time had yet elapsed for that to occur. The glueing function has obvious structural and stability advantages for the nests and inevitably continues to strengthen the nest as nestlings gain weight.

Due to the relatively charismatic nature of fungi in the genus *Marasmius* and the fact that it has been widely shown to produce rhizomorphs, many studies have assumed that the rhizomorphs found in nests represent members of this genus. *Marasmius* rhizomorphs are undoubtedly used in nests, but we suspect that future studies utilising molecular techniques will likely also reveal the use of additional groups of rhizomorph-forming fungi. We have found no studies that have methodically observed rhizomorph-containing nests after they have been abandoned by the birds to note whether or not fruiting bodies form. Koch et al. (2018) observed nests that contained *Brunneocorticium corynecarpon* post fledging, but this fungus has never been observed to form fruiting bodies under any condition. We hypothesize that in many situations, the rhizomorphs may begin to fruit post fledging. Many of the detailed studies on bird nesting behaviour cease at fledging, so very little information has been gathered to determine whether or not rhizomorphs continue to grow after nestlings leave the nest. Given the great diversity of fungal genera and species used and the diversity of birds using them, it is reasonable to expect varied associations between different combinations of species; some species may have evolved highly specialised associations with nesting birds. It is also possible that the disturbance caused by rhizomorph harvesting could trigger fruiting in the colony where the rhizomorphs were sourced. Further study is needed to fully understand what role nesting birds are playing in the dispersal of rhizomorph-forming fungi.

## Conclusions

Associations between birds and fungi significantly contribute to the maintenance and function of ecosystems worldwide and offer many avenues for future research. In this review, we cite direct examples of an array of ornithomycological associations that include 54 bird species known to eat fungi, 30 cavity-excavating birds, 176 open-nesting species that use fungal rhizomorphs and three bowerbird species that adorn their bowers with fungi. This review confirms that these associations are more ubiquitous than previously thought and are taking place in a diverse range of ecosystems.

We show that the techniques previously used in dietary analysis have biased our current understanding of the importance of fungi in bird diets. With a transition toward the inclusion of high magnification microscope analysis and/or DNA-based molecular analysis of bird diets, we will be able to substantially increase our understanding of what role bird mycophagy plays in fungal dispersal and how this and other associations impact ecosystems. We strongly encourage researchers who discuss bird-fungal associations to use standardised terms. Specifically, we recommend "mycophagy" for the action of eating fungi, with "fungus" (or "fungi") used to describe the dietary item(s). We also strongly encourage researchers to collect, voucher (lodge with a recognised herbarium) and identify, as specifically as possible, the fungus involved in the association. Adoption of these practices would allow for a much more thorough understanding of the relationships between birds and fungi.

Many tree cavity-dwelling vertebrates may depend on fungi for excavation site preparation or rely on cavity-excavating birds to excavate wood that has been softened by fungal decay. More in-depth study is needed to evaluate the full breadth of these associations. We encourage future studies on excavation site selection to utilise DNA-based surveys for fungal community characterisation alongside the standard fruiting body documentation, and we encourage longer-term work to utilise field experiments. We urge future research to include an examination of fungal secondary metabolites and how they contribute to excavation site selection and the maintenance of excavated cavities. We suggest combining fungal community identification with wood hardness data when possible. Above all, with any study about cavity-excavator excavation site selection, we advocate for the use of field controls. One cannot determine which factors contribute to the selection of an excavation site without also examining similar sites without excavations.

The majority of the 176 bird species reported to use fungal rhizomorphs are poorly studied species residing in the tropical regions of the world. Many rhizomorphs used in nests are difficult to see and are challenging to identify and thus have likely been overlooked or misidentified. There is a desperate need for DNA analysis of rhizomorphs used in nests. This could easily be accomplished by taking small samples from nests preserved in existing museum collections. With better clarity on the diversity of species used, it may be possible to assess the importance of these bird dispersal events for rhizomorph-forming fungi. Since many of these groups of fungi are important canopy litter trapping species and are cycling and retaining nutrients in the canopy, it is important that we learn more about their biology to understand nutrient cycling in tropical forests. Some of these groups of fungi seldom or never produce fruiting bodies, so it is plausible that birds may be important vectors in moving them through the canopy.

Ornithomycological associations are the subject of an emerging field. We hope this review shows how much work is still needed to fully understand the complex and multifaceted associations between birds and fungi, and we hope that our work will also serve as a springboard for increased interest in and research of these associations.

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