What We Don't Know About Slugs & Mushrooms!

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Abstract:

Very little is known about slug-mushroom interactions. In an effort to assemble preliminary base-line data for the Canadian province of Newfoundland and Labrador, we examined all locally available mushroom photographs for the presence of slugs, and all locally available slug photographs for the presence of mushrooms. A total of 43 mushroom taxa were found to be associated with 6 slug taxa. The occurrence of slugs on mushrooms generally conformed to the known geographic distribution, frequency of occurrence, and ecological preference of each slug taxon within the province. However, the list of associated mushrooms did show some notable deviations from known regional prevalence. It was clearly determined that photographs of mushrooms do not always capture the critical field characteristics of associated slugs, and vice-versa. It is thus recommended that such photographic evidence should always be supported by voucher specimens for later examination and archiving.

Key words:

Antifeedant, Arion, Carinarion, Deroceras, food, fungi, interaction, Labrador, Lehmannia, Limax, mollusc, mushroom, mycophagy, Newfoundland, repellent, slug, spore, toxin.

Introduction

In his book "Eight Little Piggies" (1993), the late Harvard University snail paleontologist, and noted evolutionist, Stephen J. Gould, told a wonderful story about exploring the Miocene sediments of Africa's Great Rift Valley with the famed human paleontologist Sir Richard Leakey. Gould noticed fossil snails everywhere, but Leakey, who had never seen a single snail in the area, had to point out the numerous fossil human bone fragments to Gould, who couldn't see them at all! Gould's point in telling the story was that it is all about knowledge-related "search image". Sometimes we must consciously shift our mental focus, and start thinking in more multidisciplinary ways, if we are to discover things that are sitting right in front of us. So it is with slugs and mushrooms. Slug hunters see slugs. Mushroom hunters see mushrooms. While both are generally aware that slugs can do serious damage to mushrooms, in practice, the specifics of the relationship go largely unnoticed, and unrecorded.

Indeed, most literature addressing the subject of slug-mushroom interaction is decidedly uninformative (e.g. Thomas, 1939; Quick, 1960; Ellis, 1969), noting merely that certain slugs eat "fungi". A notable exception is the slug volume (1907) of Taylor's exhaustive *Monograph of the Land & Freshwater Mollusca of the British Isles*: "*Limax maximus* … greedily devours fungi, which, indeed, are said to form its staple diet and to be preferred to other food … In Mr. Gain's [1891] experiments … *Boletus edulis* … were eaten with avidity. It has also been observed by Dr. [R. F.] Scharff [1891] to devour *Russula emetica*"; "Although not usually a fungus feeder, *A. agrestis* [=*Agriolimax agrestis* s.l., including var. *reticulatum* (= *Deroceras reticulatum*)] will, like the true *Limaces*, at times feed upon various kinds of fungi, poisonous and edible, *Boletus edulis*, *Amanita muscaria*, and *A. phalloides*, being especially mentioned"; "*Agriolimax laevis*" [= *Deroceras laeve*] ate "more or less freely … the fungus *Polyporus squamosus*"; "*Arion ater* … readily devoured … edible and poisonous fungi"; "*Arion subfuscus* is naturally very partial to fungi, and has been observed to frequent and feed upon *Russula fuscata* [ie. *R. fusca* = *R. integra*], as well as on the poisonous *Agaricus muscarius* [= *Amanita muscaria*]; "Dr. Scharff remarks that he has never found

Deroceras laeve and *Cortinarius mucifluus*. Photo: John E. Maunder

Figure 1

Above: Why is the above group of *Hygrocybe leata* so tattered and torn? Two slugs *(Arion subfuscus)* can be seen lurking in the shadows in the lower right corner of the photo. See close-up, to the left. Photos: Andrus Voitk.

[*Arion hortensis* s.l.] on fungi, but in confinement Mr. Gain observes that it fed readily upon *Agaricus campestris*, *Russula emetica*, and several other species."; "According to [A.] Baudon, [*Arion circumscriptus* = *Carinarion fasciatus* s.l.] is rather common in … the stem and cap of large mushrooms of which and other fungi *A. circumscriptus* is particularly fond".

Five more publications record similarly useful information. 1. Økland (1923), for Norway: "*Arion ater* [has been] not rarely … seen on fungi"; "For a long time *Arion subfuscus* was considered to feed exclusively on fungi, eating large holes especially in *Russula* and *Lactarius deliciosus*. But later on it has been stated to feed on several kinds of vegetables and even on carrion."; "*Arion circumscriptus*" [= *Carinarion fasciatus* s.l.] …"may occasionally be found on fungi". 2. Barnes and Weil (1945), for England: "the puff-ball must have, during part of the summer, formed a favourite item of the diet of the slugs, to judge from the numbers of *Limax maximus*, *Arion hortensis*, *A. subfuscus*, *Milax gracilis* and *M. sowerbyi* seen feeding upon groups of immature specimens. Toadstools of various kinds have also been observed to be eaten by slugs during the early autumn". 3. Beyer and Saari (1978), for the USA: "*Arion subfuscus* … frequently fed on fungi. Most kinds of soft-bodied fungi were eaten, but woody fungi, such as *Fomes applanatus* [= *Ganoderma applanatum*] and *F. fomentarius* were generally avoided. Softer polypores, such as *Daedalea confragosa* and *Polyporus tsugae* [= *Ganoderma tsugae*] received severe and continual damage"; "[it also ate] films of algae and fungi growing on bark." 4. Keller and Snell (2002), for the USA: in the Great Smoky Mountains National Park "*P.* [*Philomycus*] *carolinianus* was observed feeding on the gill edges and cap margins of species of *Russula* and *Lactarius* and the pores of *Laetiporus sulphureus*"; in the northwestern states "Mushrooms such as *Pleurotus ostreatus* and *Boletus edulis* are a frequent food source for [*Ariolimax columbianus*]"; "Other … basidiomycetes that are eaten [by *A. columbianus*] include species of *Pleurocybella* and *Agaricus*." 5. Frömming (1954), for central Europe: numerous mushrooms were listed as being eaten by *Limax* and *Arion*.

Figure 2

The underside of a picked *Gyromitra gigas*, showing four, small, embedded *Arion subfuscus*. Photo: Andrus Voitk.

A few additional studies have looked more generally at the food of slugs (Jennings and Barkham, 1975; Pallant, 1969, 1972), often examining what slugs will or will not eat under laboratory conditions (Getz, 1959; Rathcke, 1985; Scheidel and Bruelheide, 1999; Duthoit, 1964). However, the relationship between slugs and mushrooms is about much more than just slug food preferences.

While aerial dissemination of spores is the primary dispersal mechanism in fungi, animals also play important dispersal roles. It is well-known that the

spores of truffles and other hypogenous (ie. underground) mushrooms are spread by small mammals (Fogel and Trappe, 1978, Maser *et al.,* 1978; Johnson, 1996), and that the spores of other types of mushrooms are spread by insects and other arthropods. Indeed, a particularly detailed recent study by Lilleskov (2005) showed a wide variety of invertebrates, including arthropods, to be primary spore dispersal vectors for the terricolous mushroom *Tomentella sublilacina*, via both internal transport (in the digestive tract) and external transport (on the integument).

However, even though slugs are generally known to feed on mushrooms, vanishingly few writers have specifically implicated them in mushroom spore dispersal. A notable exception is Roberts (1998) who recently stated that intact, occasionally germinating, spores of all of the commonly eaten members of the *Russulaceae,* as well as of *Armillaria ostoyae*, *Thelephora terrestris*, members of the genera *Suillus*, *Gomphidius*, *Cortinarius*, and other unidentified basidiospores and ascospores, have been found in the fecal strings of the west coast North American mycophagous banana slug, *Ariolimax columbianus*. Turchetti and Chelazzi (1984) found evidence to suggest that the slug *Lehmannia marginata* acts as an important dispersal vector for the chestnut blight fungus *Endothia parasitica*, although whether the transported fungus propagules were carried internally, or externally, was unclear.

Not surprisingly, many fungi have developed mechanisms for either [1] attracting organisms that act as spore dissemination vectors, or [2] repelling organisms that threaten to damage their fruiting bodies.

The mechanisms which make certain sporocarps specifically attractive to mycophagous slugs remain largely unknown. We do know that mushrooms produce chemicals that attract insects (Combet *et al.,* 2006). We also know that the sense of smell is very well developed in slugs (eg. Murakami *et al.* 2004). But, that is about all.

Many slugs are able to feed with impunity on mushrooms that are fatally poisonous to most animal species, including humans (Fig. 5). However, here again, the mechanisms involved remain largely unknown.

Among the invertebrates, mycophagous species of *Drosophila* (fruit flies) have been found to have a remarkable tolerance for lethal (to humans) fungal amatoxins (Jaenike *et al.*, 1983; Jaenike, 1985). Among the vertebrates, deer have been observed feeding on the poisonous species *Amanita verna*, *A. virosa*, and *A. bisporigera*, apparently without ill effects (H. W. Keller, pers. com.). Indeed, ruminants, in general, have been shown to be considerably less affected by mycotoxins than are other mammals (Karlovsky, 1999; Hussein and Brasel, 2001).

It has become increasingly apparent that gut-living microbial and protozoan symbionts, not gut enzymes, are primarily responsible for the detoxification of mycotoxins in the digestive systems of ruminants, and

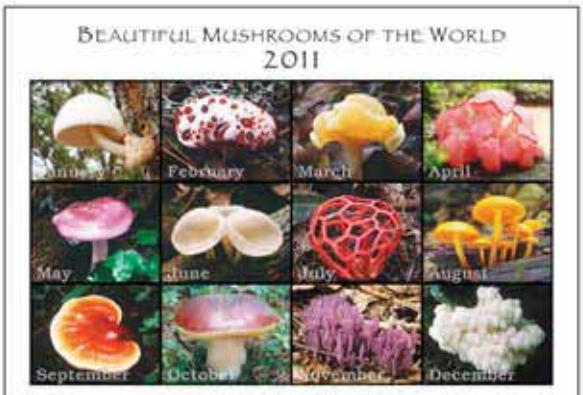

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Figure 3

Suillus cavipes, showing severe slug damage to the spore-producing structures. Photo: Andrus Voitk.

Slugs feeding on spore-producing structures. *Cortinarius stillatitius* and *Arion subfuscus* [top left], *Lactarius thyinos* and *Arion subfuscus* [top right], and *Tricholoma flavovirens* and an unidentified slug [left]. Photos: Andrus Voitk, John E. Maunder, and Andrus Voitk.

Figure 4

many other resistant animals, both vertebrate and invertebrate (Karlovsky, 1999; Hussein and Brasel, 2001). Perhaps, the mechanism of mycotoxin tolerance in slugs will also be found to involve such symbionts?

Under certain circumstances, slugs *may* actually feed upon mushroom species that are harmful to them. An example appears to be Wallis Kew's observation (*ex*. Taylor, 1907) that "*Phallus impudicus* was ... greedily devoured [by *Arion ater*], but the animals feeding upon it died soon afterwards".

Despite their heroic feeding tolerances, slugs do appear to be repelled by a number of mushroom species. Richter (1980) contributed some of the first insights into the dietary preferences of *Ariolimax columbianus,* and its aversions to certain mushrooms.

Roberts (1998) subsequently recorded that *Ariolimax columbianus* avoids or rarely samples most species in the genera *Inocybe, Telamonia, Laccaria, Collybia, Marasmius, Xeromphalina, Phellodon, Clavulina,* and *Pseudohydnum,* as well as *Hebeloma crustuliniforme*. Recently, three mushroom species, *Tricholoma magnivelare, Clitopilus prunulus* and *Clitocybe flaccida*, were specifically shown to produce chemicals that act as repellents and antifeedants to *Ariolimax columbianus* (Wood and Lefevre, 2007, Wood *et al.,* 2001, 2004). Undoubtedly, additional slug species will be found to be similarly affected by fungal repellants and antifeedants.

The foregoing account sums up virtually all that is known, or surmised, about slug-mushroom interactions. To date, there does not appear to be a single, substantial, focused account of this relationship under natural conditions. In marked contrast, there has lately been significant renewed interest in the *insects* infesting mushrooms (eg. Bunyard, 2003).

We have recently taken a modest first step towards a more detailed understanding of slug-mushroom interactions within the Canadian province of Newfoundland and Labrador. Underpinning our study is considerable baseline data on both slug and mushroom occurrence in the region. Continuing field surveys by JEM and research colleague Ronald G. Noseworthy have revealed that the Newfoundland and Labrador slug fauna remains steady at eight taxa (Table 1).

Amanita bisporigera (Destroying Angel) and *Arion subfuscus*. Photo: Andrus Voitk.

Figure 5

Only *Deroceras laeve* is considered to be (at least primarily) native; the other seven taxa have apparently been introduced over time, from Europe. In contrast, additions to the provincial mycota continue apace, largely as the result of annual mushroom forays. The cumulative total for *Foray Newfoundland and Labrador* presently stands at 956 species (Malloch, 2008). The numbers are still rising in a straight line and the 2009 foray is expected to take the total over 1000.

Methods

We reviewed all available photographs of Newfoundland and Labrador mushrooms, looking for included slug images. Similarly, we reviewed all available photographs of Newfoundland and Labrador slugs, looking for mushroom images. Most of these photographs were taken by AJV and JEM; a few were contributed. Mushroom identifications, the majority based upon professionally identified voucher specimens, in addition to photographs, were provided by AJV. Slug identifications, based solely upon the examination of the available photographs, were provided by JEM (who, along with Ronald G. Noseworthy, is currently conducting an intensive study of the terrestrial and freshwater mollusc faunas of Newfoundland and Labrador). The photographs that formed the basis of our study are archived by JEM. For the majority of mushroom species involved, voucher specimens are archived by AJV for the *Foray Newfoundland and Labrador*.

Results

Fifty-four of our photographs were found to depict "slug-mushroom interactions" (defined as any definite associations, ranging from simple physical contact to extreme slug mycophagy). A total of 43 mushroom taxa and 6 slug taxa were represented (Table 2). No mushroom taxon encountered was clearly predominant. *Arion subfuscus* (30 definite, plus 5 probable occurrences) was the predominant slug taxon. Less common were *Deroceras laeve* (9 occurrences), *Arion ater* (2 occurrences), *Limax maximus* (1 occurrence), *Deroceras reticulatum* (1 occurrence), and *Carinarion fasciatus* s.l. (1 occurrence). Five more photographs portrayed slugs that could not be identified at all, for reasons described below.

Discussion

Not surprisingly, we found that pre-existing photos of slug-mushroom interactions were relatively few. Mushroom photographers tend not to photograph specimens with slugs on them, since the mushrooms are often damaged and slugs are just a distraction. Moreover, most of our pre-existing mushroom photos were taken for the expressed purpose of mushroom documentation and were, therefore, not especially useful for slug identification, since the animals depicted tended to be somewhat out-of-focus, oriented at awkward angles, or partially submerged in the flesh of the mushroom (Fig. 6). Additionally, slug photographers tend not to photograph their subjects on three-dimensional substrates as challenging as mushrooms when critical identification is an object; therefore, very few of our pre-existing slug photos include mushrooms.

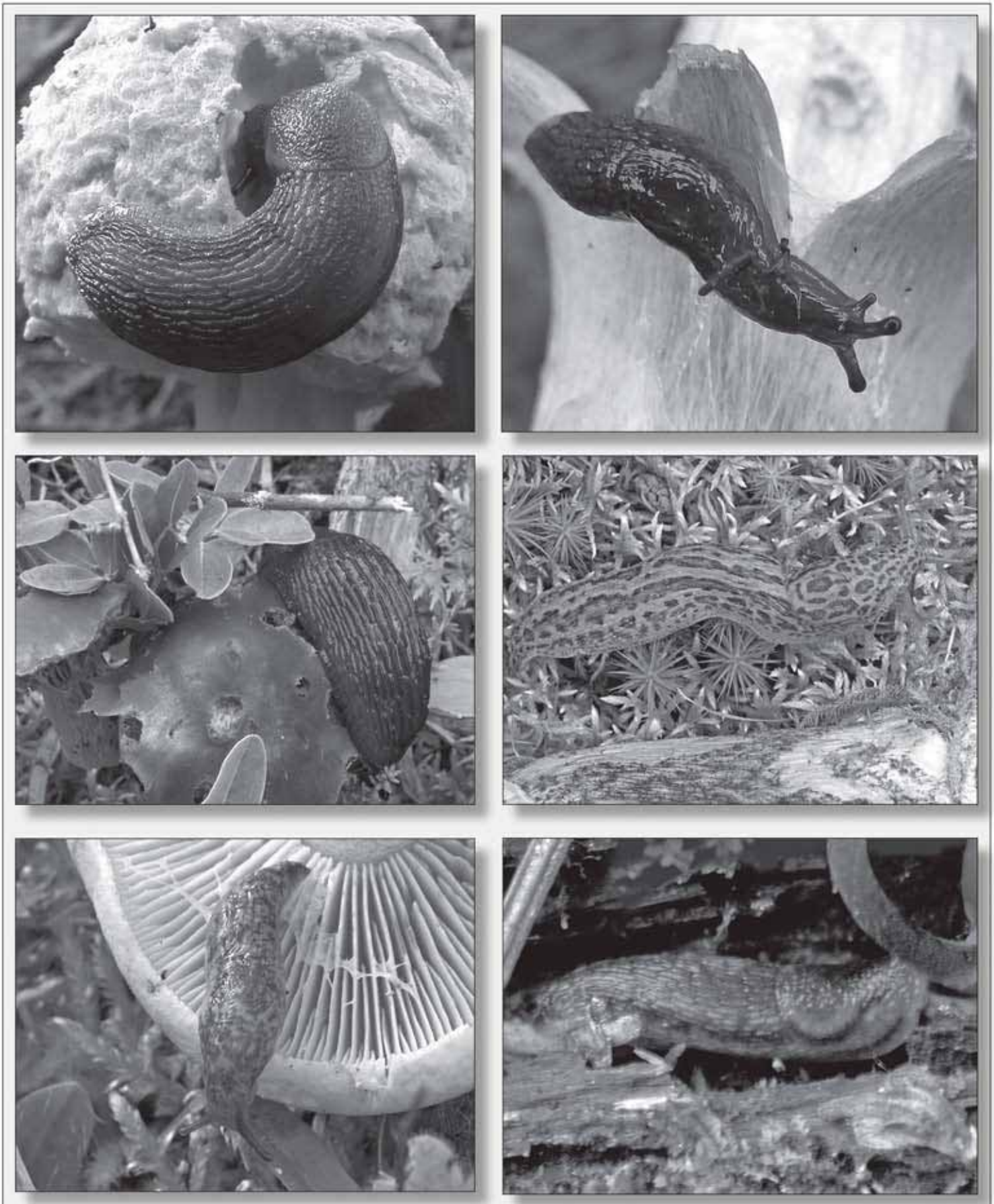
Figure 6: *Hypomyces lactifluorum* with two *Arion subfuscus* cruising through its flesh [top], and *Gyromitra gigas* with a submerged *Arion subfuscus* [bottom]. Photos: Andrus Voitk.

Figure 6

Our study clearly showed that while photography can be a very effective way of recording both slug and mushroom occurrences, the technique has very definite limits. Some slug taxa, like some mushroom taxa, are very difficult to distinguish from photos, even if such photographs are carefully taken. Standard field marks are often invisible or indistinguishable in photographs, to the point where satisfactory identifications may have to rely almost entirely upon the intangible personal insights and instincts of experts intimately familiar with the morphological and behavioral subtleties of their subjects. Unfortunately, such experts are very rare; and even they can be stumped. Thus, the collection of difficult taxa, for later detailed examination and dissection, is crucial. Ideally, of course, *all* photographs should be supported by permanent voucher specimens of both slugs and mushrooms.

Any future work will require a much more rigorous protocol, with defined temporal, geographic, and ecological parameters. The foregoing concerns notwithstanding, we believe that our preliminary data offer some useful initial insights into slug-mushroom interactions in Newfoundland and Labrador.

Our results are revealing, both for what was found and what was not. As already noted above, the most common slug recorded in our photographs was, not surprisingly, *Arion subfuscus*, a species known to be particularly common throughout the Island of Newfoundland, and also known to favor mushrooms. The relatively frequent occurrence of the (at least primarily) native *Deroceras laeve* was also expected. It too is a known mycophage, and is, province-wide, our most ubiquitous forest dweller, despite its common name "Meadow Slug". Two east coast records of *Arion ater* reflect the fact that this forest-loving species is restricted to the Avalon Peninsula on the east coast of the Island. The single west coast occurrence of *Limax maximus* is similarly consistent with the rather restricted distribution of the species on both the east and west coasts of the Island (Bateman and Burzynski, 2008). Interestingly, *Deroceras reticulatum*, which is considered to be relatively common throughout the Island, was also recorded only once; the reason probably being that this slug is primarily a denizen of open meadows (South, 1965), unlikely to be encountered frequently on mushroom forays. Indeed,



Arion subfuscus and *Amanita muscaria* [upper left], *Deroceras laeve* and *Cortinarius stillatitius* [upper right], *Arion ater* and *Cortinarius evernius* [middle left], *Limax maximus* and *Leccinum snellii* [middle right], *Deroceras reticulatum* and *Hebeloma crustuliniforme* [bottom left], and *Carinarion fasciatus s.l* and *Mycena sp. 1* [bottom right]. Photos: All A. J. Voitk, except M. Burzynski [upper right].

Figure 7

throughout its range, *D. reticulatum* does more damage to horticultural and agricultural crops than do most other slugs, having a clear preference for grain plants (Duthoit, 1964). Also recorded only once, the relatively common *Arion fasciatus* s.l. is primarily restricted to the vicinity of human habitation on the Island and is therefore less likely to be encountered during hinterland-biased mushroom forays.

Two Newfoundland slug taxa are not represented in our slug-mushroom list (Table 2) at all. *Arion distinctus*, like *Carinarion fasciatus* s.l., is primarily restricted to the vicinity of human habitation on the Island; and *Lehmannia marginata* is very sparsely distributed, primarily in coastal areas.

A casual glance at the mushroom taxa recorded in this study will provide very few surprises to those familiar with the mycota of our province. Most are familiar species, regularly encountered particularly on the west coast of the Island, which should be expected in any random photocensus. However, what may surprise are the species that were not encountered. For example, *Laccaria laccata* and *Gymnopus dryophilus*, two of the true truly ubiquitous and plentiful species found on nearly every foray list in North America were not included in our slug-mushroom list. Nor were many other species identified as common on our local forays. Have ubiquitous and plentiful species been especially successful at establishing themselves widely because they possess some manner of defense against natural enemies like slugs?

As others have also observed, mycophagous slugs do not feed on mushrooms indiscriminately, seeming to have their own preferences for individual mushroom species; preferences that do not necessarily parallel the commonness of the mushrooms available. The absence, from our slug-mushroom interaction list, of *Cantharellus cibarius*, *Craterellus tubaeformis*, *Hydnum repandum* and *Hydnum umbilicatum* is particularly striking. These four highly regarded edibles are reasonably common throughout the Island, being species that the mushrooming author (AJV) seeks out specifically for the table and thus encounters disproportionately more than other species. This suggests the possibility that there are protective mechanisms associated with these four species as well. The topic seems well worth pursuing, particularly because there may be some regional variation involved; mycophagists from the Avalon Peninsula, on the east coast of our Island, often complain about both slug and larval insect damage to chanterelles, something not an issue on the west coast.

An additional topic for future investigation might be the relative effects of introduced slugs (eg. *Arion subfuscus*), versus native slugs (eg. *Deroceras laeve*), on the native mycota.

Acknowledgements:

Special thanks to Nathalie Djan-Chékar, Henry Mann, Susan Maunder, Faye Murrin, Ronald G. Noseworthy, and Mac Pitcher, for criticizing early drafts of this paper. Thanks also to reviewer Harold W. Keller who provided useful suggestions for improving the submitted manuscript. Further thanks to Michael Burzynski, Jennifer Woodland, and Jamie Graham for contributing additional photographs.

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Family	Scientific name	Common name
Agriolimacidae	*Deroceras laeve*	Meadow Slug
	Deroceras reticulatum	Grey Field Slug
Arionidae	*Arion ater*	Black Arion, Black Slug
	Arion distinctus	Darkface Arion, Darkface Slug
	Arion subfuscus	Dusky Arion, Dusky Slug
	Carinarion fasciatus sensu lato (s.l.)	Forest Arion, Forest Slug
Limacidae	*Lehmannia marginata*	Tree Slug
	Limax maximus	Giant Garden Slug, Great Slug, Leopard Slug

Table 1. Slug taxa recorded from Newfoundland and Labrador. *Carinarion fasciatus* is considered here in the broad sense in light of the recent conclusions of Geenen *et al.* (2006) which show that neither of its formerly recognized subtaxa *(fasciatus s.s., silvaticus,* or *circumscriptus)* is monophyletic, and, further, that the taxonomy of this once comfortable little group is now completely unresolved.

Mushroom	Slug
Amanita bisporigera	*Arion* cf. *subfuscus*
Amanita flavoconia	unidentified (image inconclusive)
Amanita muscaria (2)	*Arion subfuscus*
	unidentified (image inconclusive)
Armillaria ostoyae	*Arion subfuscus*
Catathelasma ventricosa (2)	*Arion subfuscus*
	Deroceras laeve
Cortinarius evernius	*Arion ater*
Cortinarius mucifluus	*Deroceras laeve*
Cortinarius stillatitius (3)	*Arion subfuscus*
	Arion subfuscus
	Deroceras laeve
Galerina sphagnicola	*Arion subfuscus*
Gomphus clavatus	*Arion* cf. *subfuscus*
Gyromitra esculenta	*Arion subfuscus*
Gyromitra gigas (2)	*Arion subfuscus*
	Deroceras laeve
Gyromitra leucoxantha	*Arion subfuscus*
Hebeloma crustuliniforme	*Deroceras reticulatum*
Hygrocybe laeta	*Arion subfuscus*

Table 2. Mushroom-slug associations, by taxon, in this study. Numbers in parentheses indicate the number of separate mushroom or mushroom-clump occurrences (where the number is greater than 1).

Table 2 continued.

Hygrocybe persistens	*Arion subfuscus*
Hygrophorus pustulatus	*Arion subfuscus*
Hypomyces lactifluorum	*Arion subfuscus*
Inocybe sp.	*Deroceras laeve*
Lactarius deceptivus	*Arion subfuscus*
Lactarius deterrimus	*Arion subfuscus*
Lactarius thyinos (3)	*Arion subfuscus*
	Arion subfuscus
	Deroceras laeve
Lactarius sp.	*Arion ater*
Leccinum snellii	*Limax maximus*
Lentinus lepideus	*Arion* cf. *subfuscus*
Lycoperdon perlata	unidentified (image inconclusive)
Lycoperdon pyriforme	*Arion subfuscus*
Megacollybia platyphylla	*Arion subfuscus*
Morchella elata (2)	*Arion subfuscus*
	Arion subfuscus
Mycena sp. 1 [a species resembling *M. overholtsii*] (2)	*Arion subfuscus*
	Carinarion fasciatus s.l.
Mycena sp. 2	*Deroceras laeve*
Pluteus cf. *cinereofuscus*	*Arion subfuscus*
Rhodocollybia prolixa var. *distorta*	*Arion subfuscus*
Russula cf. *aeruginea*	*Arion subfuscus*
Russula decolorans	*Arion subfuscus*
Russula paludosa (2 definite and 1 cf.)	*Arion subfuscus*
	Arion subfuscus
	Arion subfuscus
Russula sp.	*Deroceras laeve*
Stropharia caerulea	*Arion* cf. *subfuscus*
Stropharia thrausta	*Arion subfuscus*
Suillus cavipes	unidentified (image inconclusive)
Tricholoma flavovirens	unidentified (image inconclusive); apparently either *Arion subfuscus* or *Limax maximus*
Tricholoma scalpturatum	*Deroceras laevo*
Tricholoma vaccinium	*Arion* cf. *subfuscus*

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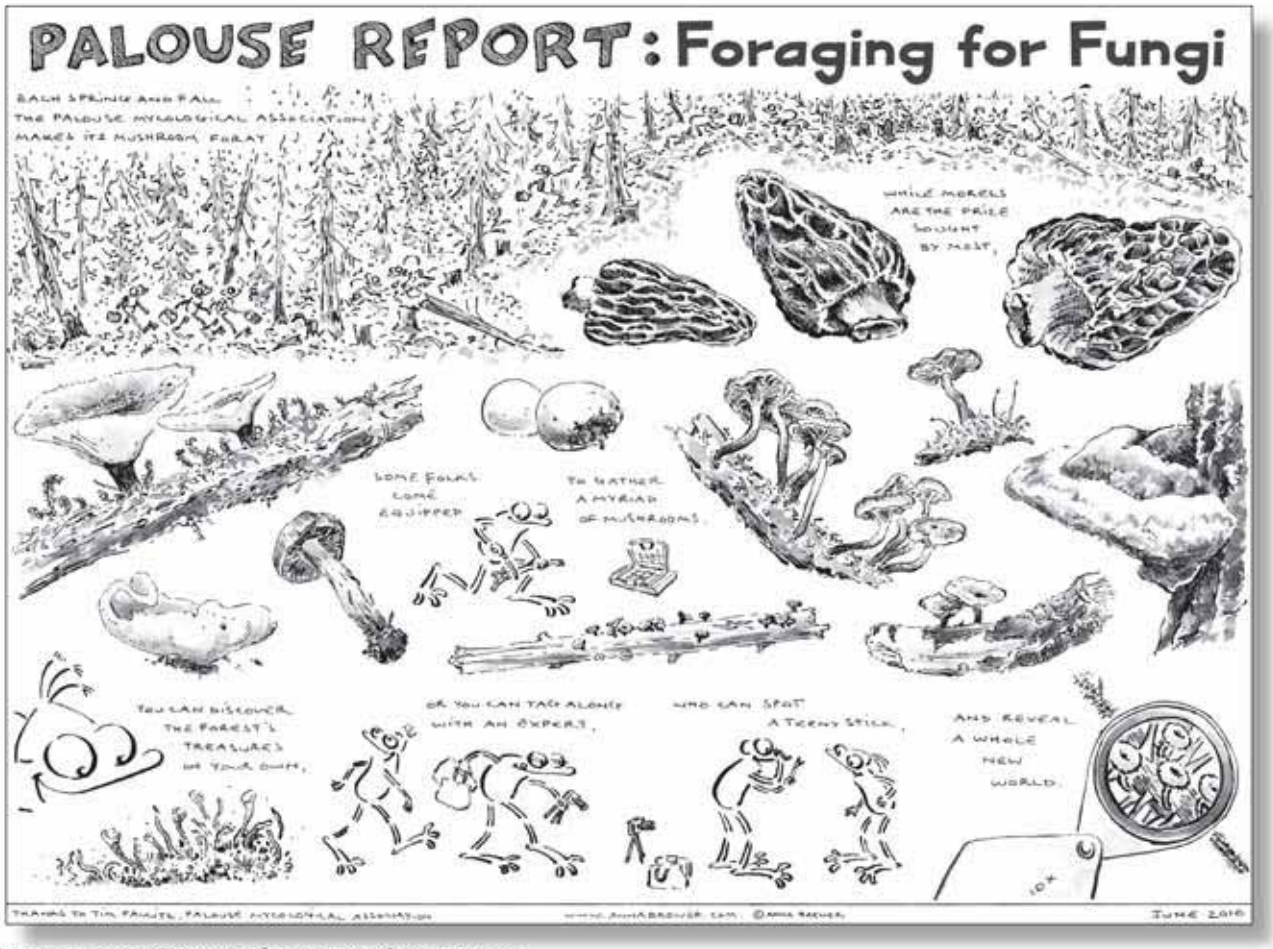

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