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Gut-retention time in mycophagous mammals: a review and a study of truffle-like fungal spore retention in the swamp wallaby

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ABSTRACT

Variation in the gut-retention time of macrofungal spores influences the distance to which spores are dispersed by mycophagous (fungus-feeding) mammals and is of interest in examining mammal-fungal interactions. In reviewing published studies of fluid and particle (including macrofungal spore) digesta gut-retention times in ground-dwelling mycophagous mammals, weighted mean retention times (MRT) were found to range 6.6–55.5 hr. Among macropodoid marsupials, fluid and small particle weighted MRT was longer in mycophagous species than non-mycophagous species but statistical support for this difference was weak (estimated mean difference 7.2 hr; 95 % CL [−0.8, 15.1] hr). Gut-retention of truffle-like (below-ground fruiting) fungal spores was examined in the swamp wallaby (*Wallabia bicolor*), a browsing macropodid marsupial that regularly eats macrofungal fruit-bodies. Two wallabies of different body weights were examined in a captive feeding trial. MRT of marker spores were 26.9 hr and 35.1 hr for the larger and smaller animal respectively. A small number of marker spores were found in faecal pellets up to 69 hr after ingestion, suggesting that there is potential for long distance dispersal of fungal spores by swamp wallabies. The studied swamp wallabies probably carry fungal spores for similar times to smaller mycophagous marsupials, including the strongly mycophagous potoroids. Further studies of spore gut-passage, including MRT, in mycophagous mammals would help clarify differences among species and groups of species.

Introduction

Interactions between mycorrhizal fungi, host plants, and mammals influence forest ecosystem function. Trees and other woody plants form biotrophic symbioses with ectomycorrhizal (EM) fungi (Brundrett 1991; Read 1991). Most EM fungi produce fruit bodies (sporocarps) and these are an important food resource for many mammals (Fogel & Trappe 1978; Claridge & May 1994; Claridge *et al.* 1996; Maser *et al.* 2008). Mammals are vital spore dispersal agents, particularly for truffle-like (below-ground fruiting) sporocarpic fungi that do not actively discharge their spores (Fogel & Trappe 1978; Claridge & May 1994; Claridge *et al.* 1996; Johnson 1996; Reddell *et al.* 1997; Bougher & Lebel 2001; Maser *et al.* 2008). Spore dispersal is important for both maintenance of genetic flow within and between fungal populations and for colonization of new habitats (Bruns *et al.* 2009). For mycorrhizal host plants and the plant-soil system, maintenance of a diverse

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mycorrhizal fungal community maintains resilience through resource partitioning and competition amongst fungi (Perry *et al.* 1989; Deacon & Fleming 1992; Bruns 1995). Rapid seasonal turnover of plant root tips results in strong local-scale competition among mycorrhizal fungi for this resource (Bruns 1995). By disseminating spores in their faecal pellets, mycophagous (fungus-feeding) mammals help maintain fungal diversity within their home range (Maser *et al.* 2008). While most mycophagous mammal movement occurs within a frequently-used area (home range), occasional long distance movements occur and may be significant spore dispersal events.

Few mycophagous mammals remain on the New England Tableland of north-eastern New South Wales; bettongs, potoroos, and bandicoots have largely been extirpated from the modified landscapes of this region in the period since European occupation (Jarman & Vernes 2006). However, the swamp wallaby, *Wallabia bicolor*, a plant browser and regular mycophagist is resilient in these EM-forested landscapes. Swamp wallabies consume a diversity of truffle-like fungi year-round (M. Danks, unpublished data; Claridge *et al.* 2001; Vernes & McGrath 2009; Vernes 2010) and may contribute to the maintenance of vital mammal-truffle-plant relationships in these simplified communities.

Gut-retention time of fungal spores in mycophagous mammals is of interest in examining mammal-fungal interactions as, along with movement patterns, variation in gut-retention influences the distance to which spores may be dispersed (Cork & Kenagy 1989b). Gut-passage is influenced by body mass, gut morphology and diet (Cork & Kenagy 1989b; Hume 1989). Most studies examining mammalian digesta passage have held study animals in metabolism cages and used chemical or physical markers to illustrate the passage of fluid or particle digesta phases (e.g. Calaby 1958; Warner 1981a; Hume & Carlisle 1985; Sakaguchi & Hume 1990; Moyle *et al.* 1995; McClelland *et al.* 1999; Gibson & Hume 2000; Pei *et al.* 2001). Gut-passage has rarely been studied in free-ranging mammals on a natural diet, making it problematic to interpret the ecological meaning of reported gut-retention times. Gut-retention time of fungal spores has also received relatively little attention. The few studies that have directly assessed gut-retention of fungal spores have examined mycophagous rodents; for example, the giant white-tailed rat, *Uromys caudimaculatus* (Comport & Hume 1998), the golden-mantled ground squirrel, *Spermophilus saturatus*, and the deer mouse, *Peromyscus maniculatus* (Cork & Kenagy 1989b). The present study is the first to assess spore gut-passage in a mycophagous mammal on a semi-natural diet, and the first to measure spore gut-passage in a macropodoid marsupial.

In this paper I: (1) review published data on gut-retention times in mycophagous mammals, including macropodids (wallabies), potoroids (potoroos and bettongs), peramelids (bandicoots), rodents (squirrels, voles, and mice), and possums; and (2) examine the time taken for native truffle-like fungal spores to pass through the gut of swamp wallabies. I use gut-retention times to broadly examine the spore dispersal role of these mammals rather than to compare their digestive efficiency. Factors influencing digesta passage are discussed in relation to fluid, small particle, and macrofungal spore gut-retention time in the swamp wallaby and other mycophagous mammals. Fluid and particulate digesta pass through the digestive tract as different digesta phases (Faichney 1975). Spores of EM fungi are thought, due to their small size of generally <20 μm diameter, to move through the gut with the fluid phase although some spores may remain attached to sporocarp fragments and pass through the gut with the large particle phase (Comport & Hume 1998). Spore gut-retention time in the swamp wallaby is expected to be most similar to fluid gut-retention times reported for other browsing and grazing wallabies as, despite their smaller size, these animals are most similar to swamp wallabies in terms of diet and gut morphology.

Materials and methods

Published data on digesta gut-passage in mycophagous mammals

Published data on macrofungal spore, fluid, and particle digesta mean retention times (MRT) in mycophagous mammals were collated. Comparisons among macropodoid marsupials (macropodids – kangaroos and wallabies; and potoroids – potoroos, bettongs and rat-kangaroos), both mycophagous and non-mycophagous, were also made. The 50 % excretion time (ET) measure, while not the same as MRT, is considered similar enough for broad comparisons of gut-retention times to be made (Stevens & Hume 1995), so 50 % ET measures were included in this summary where MRT was not reported. Both measures are referred to here as 'gut-retention time'. Several researchers provide information on digesta passage in mycophagous mammals but do not report MRT or 50 % ET (e.g. Calaby 1958; Hume & Carlisle 1985; Richardson 1989), preventing comparison with the present study, so these studies were not included in the summary.

In studies of large particle (size ranges between 300–1200 μm diameter) MRT, various chemical or radio-isotope markers, including chromium mordanted onto cell-wall constituents (Cr-CWC), dyed leaf particles, and ^{103}Ru-labelled tris-(1,10 phenanthroline)-ruthenium (11) chloride (Ru-P) leaf particles were utilised. Fluid digesta MRT was assessed using either cobalt-ethylenediamine tetra-acetic acid (Co-EDTA), or the ^{51}chromium complex of ethylenediamine tetra-acetic acid (Cr-EDTA). The marker used can influence the measured rate of passage of digesta. For example, Ru-P migrates from large to small digesta particles within the gut of sheep (Faichney & Griffiths 1978; Egan & Doyle 1984) and macropods (Freudenberger & Hume 1992) so that MRT of large particles may be underestimated using this marker. Cr-EDTA may not completely associate with the fluid phase (Faichney 1975), while Co-EDTA associates almost exclusively with fluid (Udén *et al.* 1980). Additionally, the fibre content and particle size distribution of the experimental diet, frequency of feeding, and animal activity levels will also influence digesta gut-passage and therefore measures of MRT. Sakaguchi & Hume (1990) reported small (<75 μm diameter) particle MRT and compared passage with that of fluids and larger (300–600 μm) particles. The fine particles passed through the gut with the fluid digesta phase. Therefore, I have assumed measures of fluid digesta passage to be measures of the passage of both solutes and small particulate digesta (<75 μm).